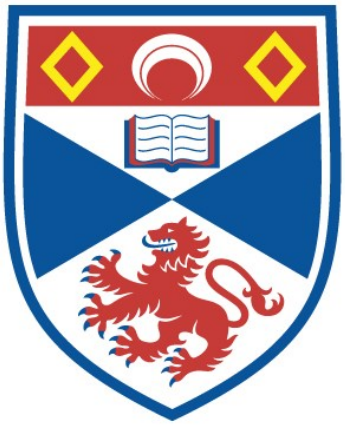
THE AUTECOLOGY OF PYLAIELLA LITTORALIS (L.) KJELLM. AT ST. ANDREWS, SCOTLAND WITH ADDITIONAL INFORMATION ON THE LIFE CYCLE OF PYLAIELLA RUPINCOLA (ARESH.) KYLIN

George Russell

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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The Autecology of *Pylaiella littoralis* (L.) Kjellm.

at

St. Andrews, Scotland

with additional information on the life cycle

of

Pylaiella rupincola (Aresch.) Kylin.

by

GEORGE RUSSELL, B.Sc.

A Thesis submitted to the University of St. Andrews for the Degree of Doctor of Philosophy.

Department of Botany,
St. Salvator's College,
University of St. Andrews.

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Declaration.

I hereby declare that the following Thesis is based on the record of work done by me, that the Thesis is my own composition, and that it has not previously been presented for a Higher Degree.

The research was carried out in the Gatty Marine Laboratory of the University of St. Andrews under the direction of Dr. M.C.H. Blackler.

Certificate

I certify that George Russell, B.Sc., has spent nine terms of Research Work under my direction and that he has fulfilled the conditions of Ordinance No. 16 (St. Andrews) and that he is qualified to submit the accompanying thesis in application for the Degree of Doctor of Philosophy.

Director of Research.

Career.

I matriculated in the University of St. Andrews in October 1952, and my course of study led to graduation in July 1956 with Honours of the First Class.

I was awarded a Carnegie Trust Post-Graduate Research Scholarship from 1st October 1956 and was admitted as a Research Student of the University of St. Andrews under Ordinances 16 and 61 as from 9th November 1956. During the tenure of the Scholarship I undertook the research now being submitted for the Ph.D.

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I wish to acknowledge my indebtedness to my supervisor, Dr. M.C.H. Blackler, who has given constant and helpful advice throughout the course of this work and in preparing it for presentation.

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TABLE OF CONTENTS

CONTENTS (cont.)

CONTENTS (cont.)

I. INTRODUCTION

Historically Pylaiella littoralis (L.) Kjellm. is most important, for it was on this filamentous species of the Phaeophyta that Knight (1923) first produced cytological evidence of meiosis in the unilocular sporangium. This event aroused interest, not only in Pylaiella, but in the Ectocarpaceae in general. The result of subsequent investigation, however, showed the species to vary considerably in its life cycle from that described by Knight for the Isle of Man. For example, detailed descriptions from the West Coast of Sweden by Kylin (1933) and from Heligoland by Damman (1930) differ both from it and from one another. Since 1937, interest in the species has apparently decreased but the problems raised by the earlier work remain. It was therefore with a view to reappraising the species both from the study of its life cycle and its ecology that the present investigation was undertaken.

The genus Pylaiella was founded by Bory de Saint Vincent in 1823 who named it after Bachelot de la Pylaie. Kjellman (1872) refers to the genus as Rylaiella and gives an extremely detailed account of the nomenclature. In this account he describes the species of Pylaiella as being previously included in such genera as Ectocarpus,

Spongomorpha and Ceramium. Ectocarpus was probably the commonest genus into which the species were placed and certainly Harvey (1846-51) describes Pylaiella littoralis as Ectocarpus littoralis. The specific name is derived from the Conferva littoralis of Linneus. The Linnean specimens, unfortunately, have not been examined and from the literature it would appear that there is considerable confusion as to which modern species is or are contained within that designated by Linneus. Setchell and Gardner (1925) in their short review of the nomenclature of P. littoralis consider it fairly certain that Linneus may have collected the species but at the same time had no concrete conception of it. This seems the most sensible interpretation.

The genus Pylaiella is found among the primitive, unspecialised algae in classifications of the Phaeophyta. It belongs to the order Ectocarpales and to its simplest family, the Ectocarpaceae. In morphology it is very similar to the genus Ectocarpus from which it is separated on grounds of differences in the positioning of the sporangia, those in Ectocarpus being borne terminally on short branches, While those in Pylaiella are found in an intercalary position. The two genera also possess chromatophores of different shape.

Pylaiella shows a typically heterotrichous growth with the erect system more luxuriantly developed than the prostrate, at least in the adult thallus. Its reproduction is also fairly simple, resulting in an alternation of what are normally morphologically identical generations. The sporophyte is diploid and forms unilocular sporangia, the first nuclear division in the sporangial mother cells being meiotic. These unilocular sporangia contain biflagellate, haploid zoospores which settle down and develop eventually into a gametophyte bearing plurilocular gametangia alone. Such plurilocular gametangia release similar biflagellate gametes which fuse, and the resulting zygote, on germination, gives rise to the sporophyte. The sexual reproduction is therefore isogamous. Both generations can reproduce themselves, the sporophyte by means of diploid zoospores formed in accessory plurilocular sporangia, and the gametophyte by parthenogenetic development of gametes.

Although similar to the species of Ectocarpus in many respects, P. littoralis is the more convenient subject of an autecological study for several reasons. Its more or less strictly littoral distribution and relatively large size make it easy to collect at low water of even the poorest neap tides. The intercalary position of its sporangia makes quick distinction from the species of

Ectocarpus possible and as it is the only species of Pylaiella recorded for the British Isles, identification is no difficulty. Lastly, the well known variation of the species in its life cycle, in the size and appearance of its individuals and in the diversity of its habitats, make it a subject of more than ordinary interest and importance.

The aims of this investigation are therefore several fold, to examine the distribution of P. littoralis in all its habitats at St. Andrews, to assess and where possible measure the environmental conditions affecting these habitats and to identify the more important associated species of the flora, and to a small extent of the fauna. They are also to discover the life cycle of the species and to find out how far this is affected by environmental conditions. Lastly, they are to investigate the variety of form presented by P. littoralis and to attempt to explain this in terms other than taxonomic.

II. DISTRIBUTION OF P. LITTORALIS

1. Northern Hemisphere.

(a) European. The species occurs commonly on most European coasts, Atlantic, North Sea and Baltic. It is also found in Mediterranean waters and Damman (1930) records it

for the Adriatic. Van Hoeck (1958) mentions a good growth of Pylaiella at Hoek van Holland on the Dutch coast and Damman again studied the species at Heligoland. On Scandinavian coasts it appears that P. littoralis is again a common alga. Waern (1952) finds it at the Öregrund Archipelago on the east coast of Sweden and on the shores of the Gulf of Bothnia. Du Rietz (1941) working a little further south at Kalmarsand also records the species as do Kylin (1947) for the west coast of Sweden and Sundene (1953) for Oslofjord. It is also a common species in the flora of west Norwegian shores as was observed by Levring (1937) and again is described by Børgesen (1902) in his Botany of the Faeroes.

(b) Atlantic. In the report of the second Norwegian Polar expedition in the "Fram" from 1898-1902 there are two references to Pylaiella littoralis. The species was observed in mid-summer at latitude 68°42' North and again at 78°18' N., the latter being the northernmost record for the species. However, it is probably a regular feature of the sub-arctic marine flora, for Jonsson (1911) notes it on the east coast of Greenland, at latitude 67°16' N.

Taylor (1957) studying the species on the North-East coast of North America observed it growing commonly at Ellesmere Island, Devon Island, Baffin Island, Hudson Bay, James Bay, Hudson Strait, Labrador, Newfoundland and on all

shores south to New Jersey. Farlow (1891) worked on the more southern parts of Eastern North America and records it south from New England.

(c) Pacific. On the Pacific coast of North America P. littoralis is equally widely distributed. Setchell and Gardner (1925) observed it from San Pedro in Southern California to the Bering Sea, a range confirmed by Smith (1943). From the latter's observations it seems that the species is nearing the southernmost limit of its Pacific distribution in South California, and at Monterey he records it only once. At the same latitude in the Atlantic ocean lie the Canary Islands and Børgesen (1927) failed to record the species there.

It will therefore be seen from these accounts that P. littoralis has a wide distribution over most Northern shores within the latitudes 40° and 70° N. and is, in all probability, circum-polar within these limits.

2. British Isles.

From the reports that are available it seems a safe assumption that P. littoralis is a common alga on all British shores. For example, in Scotland, Gibb (1939) finds it in the Firth of Clyde at the Great Cumbrae as does Campbell at Uig in the Outer Hebrides while examination of herbarium sheets in the British Museum show specimens from Granton,

Invergordon, Banff, Cromarty and Oban.

During the present investigation material has been examined which was collected from the east coast of Ireland, near Dublin and the species has been observed growing very abundantly on the west coast at Galway. Rees (1935) examined in detail the associations of marine algae on the shores of Lough Ine and also records P. littoralis of frequent occurrence.

Knight and Parke (1931) find it abundant on the Isle of Man as does Rees (1928) for Gower and Aberystwyth on the south and east coasts of Wales, respectively. Also one of the British Museum herbarium sheets bears specimens collected at St. Bride's Bay, Pembrokeshire.

The species seems equally frequent on the shores of England. The same herbarium collection contains specimens from Ilfracombe on the west coast, from Torquay, Sidmouth, Weymouth and Studland on the Channel coast, while Chapman (1930) finds it commonly on the east coast at Norfolk and the herbarium of Batters contains specimens from Berwick on Tweed.

Pylaiella littoralis is therefore of common occurrence and widespread distribution over the coasts of the British Isles.

III. THE GENERAL MORPHOLOGY OF P. LITTORALIS.

Pylaiella littoralis is typical of the filamentous Ectocarpaceae in that its growth is directed into two planes, the horizontal and the vertical. The creeping portion develops first from the germinating zoospore and consists of a mass of much branched filaments containing rather long cells of small diameter. These cells possess few or no chromatophores and are usually quite colourless. The function of this part of the thallus is two fold. It is first to anchor the plant to its substratum and second to bear the erect systems. The latter are borne at irregular intervals on the surface of the basal systems and arise, apparently, by simple branching of a prostrat filament. About one month after germination the development of the erect system predominates over that of the creeping portion and at this time the growth in the basal system is much slower than in the other. This process is maintained and when the plant has reached full size, which is probably a length of about 10 cm., prostrate growth has practically ceased.

The filaments which form the erect system very early in development begin to twine round one another, chiefly in a clockwise direction. The filaments become very closely apposed and together form a rope-like structure usually called the cable strand. This strand may branch several times in the body of the adult thallus and may, in some plants, reach a thickness of 5 mm. When well developed it gives the Pylaiella

frond a greater strength and allows it to take on a more or less permanent and characteristic shape. Poor cable development produces a rather shapeless, wispy and disorganised thallus.

The filaments that form the bulk of the frond area are produced from the cable strand and form secondary and tertiary branches in great profusion, giving the frond a characteristic fan shape when spread out. The branch tips in an actively growing plant habitually narrow in diameter to form hairs. Growth in the branches continues throughout the life of the plant and is brought about by cell divisions in certain well marked zones of the filaments. The average vegetative cell in Pylaiella is about one to one and a half times as long as broad, but in certain parts groups of about ten cells occur with lengths of only one third of the diameter. These are the areas of active growth, and such areas can be seen in various positions on actively growing filaments. The growth is therefore not strictly trichothallic. (Fig. 12)

In none of the plants examined during the investigation was there any evidence that the branches were produced in any pattern. Occasionally, it seemed, that a tendency towards opposite or secund branching was found, but close examination involving counting of the branches concerned showed this to have no real basis.

The average vegetative cell, at full development, has a

diameter of about 27μ, although the range is probably from 35μ in the oldest cells down to 12μ in branch tips. The cell wall is about 2.5μ thick and is in two layers, a thin inner one of cellulose with a thick outer part which seems to consist mainly of algin. Lining the inner wall is the layer of cytoplasm containing the chromatophores. These chromatophores are very numerous, are generally discoid in shape and always found in close association with small darkly staining pyrenoids (Fig. 13,14)

Fucosan, a tannin-like substance, is often produced in the cytoplasm and takes the form of irregularly shaped opaque bodies. Fucosan is formed in greatest quantity in plants kept in the dark and was often present in sufficient amounts to obscure cellular details.

Each vegetative cell in Pylaiella is provided with a single nucleus. This usually occupies a central position and is connected with the parietal cytoplasm by several prominent strands. At the resting stage, the nuclei are slightly subspherical in shape and contain a single prominent and darkly staining nucleolus. Chromatin material is usually visible as a faint and ragged network.

In Pylaiella two types of sporangia are found, the unilocular and the plurilocular, but in contrast with the other filamentous brown algae, these are almost always borne in an intercalary position.

The unilocular sporangia (Fig.15,16) are barrel shaped structures, slightly broader than long, the average dimensions being 32μ in breadth by 30μ in length. As in the vegetative cells, however, these figures can show considerable variation. The sporangial wall is a little thicker than that of a vegetative cell, (usually about 3μ) although in constitution it does not seem to differ.

At maturity, each unilocular sporangium forms a little swelling or papillum on its side. When the time for zoospore release approaches the wall at the tip of this swelling disrupts. This is presumably accomplished by imbibition of water and causes a small pore to be formed through which the biflagellate zoospores are discharged. These ejectory papilla usually project out from the sporangial wall for a distance of 3μ. The zoospores, of which there are about a hundred in each sporangium, are described in a later part of the text.

Unilocular sporangia are found in chains of up to thirty-three in number and are generally formed in greatest profusion during winter. Occasionally such sporangia can be found divided into two compartments by a longitudinal wall, but this is a comparative rarity.

When a unilocular sporangium dehisces, the remaining wall is not usually strong enough to bear the distal part of the filament, and this eventually breaks off. In this event the proximal part continues growth, and a young shoot can often

be seen growing through the empty walls of an old sporangium. This breaking off at an empty sporangium leaves the branch tip very much blunted and consequently in a fertile plant there are usually few terminal hairs.

Plurilocular reproductive structures occur in Pylaiella and are of two morphological types, depending largely on function. If asexual, they are almost always intercalary in position but if sexual, then more often than not are borne terminally (Fig.17,18,19).

Terminal plurilocular structures are very similar to those of Ectocarpus both in size and shape, being broad at the base and tapering to a point, though the tip of such a structure was never observed to terminate in a hair. Dehiscence is accomplished by breakdown of the loculus wall at the tip of the structure and the gametes or zoospores are released one after the other from the top and centre first and ultimately from the outer and basal loculi. In shape, the intercalary sporangia usually form an irregular oblong. This irregularity of shape may become exaggerated so that the sporangium becomes branched, while in rare cases, zoospores have been observed to germinate in situ producing a completely distorted structure. Normally a mature intercalary sporangium has a regular diameter of about 35 to 40μ and a length of up to 350μ. Dehiscence is brought about by the appearance of one or more pores in the sides of the sporangium and the zoospores

are released one after the other in a manner identical with that in the terminally borne structures.

These are the chief features in the general morphology of P. littoralis.

IV. THE LIFE CYCLE OF P.LITTORALIS.

1. Review of Literature.

A great deal of confusion existed among early workers on the life histories of algae such as Pylaiella. This arose solely from a misunderstanding of the function of the two types of sporangium. When Knight (1923) revealed that plants bearing plurilocular structures only, were gametophytes and that meiosis occurred in the development of the unilocular sporangium, it seemed that the rule for the life cycle had been established, not only for Pylaiella but also for the other members of the Ectocarpaceae. Working at the Isle of Man she found that nearly all her Pylaiella material was epiphytic and that the first growth of plants appeared on Ascophyllum nodosum in early spring. These were gametophytes and the gametes released from the plurilocular gametangia fused, germinated and grew as a new wave of plants on Fucus vesiculosus. These were sporophytes and bore unilocular sporangia almost exclusively although very occasionally accompanied by a few plurilocular sporangia. The latter were accessory sporangia in the development of which no meiosis takes place and so the zooids produced by

them merely reproduced the sporophyte. This they did in mid- to late summer and the result was the appearance of a third wave of sporophytes (again almost exclusively bearing unilocular sporangia) this time on Fucus serratus. She found that most plants were removed by storms during the winter but a few sporophytes persisted until the spring when the zooids released from their unilocular sporangia could again provide the source of a new gametophyte generation.

This seemed a complete enough explanation until the question was raised as to what happened in regions lacking the important host plants. In Heligoland Ascophyllum nodosum is uncommon and it was here that Damman (1930) collected material for her study of Pylaiella. She found that even when Ascophyllum nodosum was present the Pylaiella rarely occurred as an epiphyte but seemed to prefer Fucus spp., and grew also in large numbers on stones and rock surfaces. This material mostly bore unilocular sporangia and Damman cultured the zoospores released from them. These, after germination, gave rise to plants bearing unilocular sporangia alone, or both types simultaneously. Cytological examination of the Heligoland material revealed a diploid chromosome number of 24 (Knight, 2n = 18 - 20) and a reduction division in unilocular sporangia development. As no fusions were seen between the zoospores from the latter she concluded that haploid plants (i.e. gametophytes) could and did produce unilocular sporangia, at least on Heligoland.

This much more flexible interpretation of the life cycle resulted in a fresh interest in the species and three years later Kylin (1933) published his work on the Pylaiella growing on the Swedish West coast, near Kristineberg. He may have had some difficulty with the cytology for although he states that meiosis occurs in unilocular sporangium development no data on nuclear division or chromosome number is provided, the life cycle being described on the basis of the types of sporangia borne by successive plants. Kylin observed that small plants bearing plurilocular sporangia only could be found from April to June growing on Sertularia pumila (now Dynamena pumila) which in turn was epiphytic on Ascophyllum nodosum. They were the gametophytes and gamete fusion resulted in the growth of a race of sporophytes. These bore unilocular sporangia exclusively and occurred as epiphytes directly on fronds of Ascophyllum nodosum or alternatively on Fucus vesiculosus or Fucus serratus. Sporophytes were obtainable all year round but were at maximum development in winter.

In 1937 Kylin again published on the same subject and after studying Pylaiella in the same area, after four more years had no modifications to make to the above described cycle. He had, however, spent some time investigating the lithophytic growths of Pylaiella and had noted that in nature all such plants regularly bore only unilocular sporangia and

very rarely both types simultaneously. He isolated zoospores from the unilocular sporangia of the plants, placed them in a culture solution and noted that the resulting generation formed unilocular sporangia only. This prompted him to rename the lithophytic Pylaiella, Pylaiella rupincola (Aresch.) Kylin and to retain the P. littoralis for those plants which showed alternation of generations, or more exactly, in type of sporangia. He deduced that the lack of alternation in P. rupincola was due to inhibition of meiosis in the development of unilocular sporangia and suggested that Damman's unusual results were due to her confusion of the two species, a view which has received support from Fritsch (1942). He also tentatively suggested that P. littoralis is a tetraploid species as compared with the diploid P. rupincola.

These are the three main contributions to the life cycle of P. littoralis and not one holds entirely true for St.Andrews. In this area the bulk of the population is probably epiphytic but there is also a strong development of lithophytic communities. It is therefore convenient to discuss the two separately.

2. Field Observations.

(a) Epiphytic Pylaiella.

Epiphytic Pylaiella can be found all the year round but is undoubtedly at maximum development in the summer when its range of habitats is from M.H.W.N.T. to the upper parts of the

Laminaria zone. In October young plants can be found on Fucus ceranoides on which they persist until July. These plants bear unilocular sporangia only, throughout winter and summer. In early spring, usually about March, young plants are also found on Fucus vesiculosus (easily the commonest host in the St. Andrews area) and these appear to bear plurilocular sporangia only but close examination reveals that they bear, in fact, a few unilocular sporangia along with them. During summer these plants spread to F. serratus, Laminaria digitata, and other hosts but in sporangia formation they remain the same, all bearing both types with the plurilocular dominant. It is worth while noting that at St. Andrews, Ascophyllum nodosum is a relatively uncommon host for Pylaiella, but examination of such Pylaiella plants shows that all bear both types of sporangia simultaneously.

Autumn gales remove all but a few of these plants, but in October the species reappears growing in pools at high water mark. The plants are usually epiphytic on Fucus vesiculosus or Cladophora rupestris, but in either case they form unilocular sporangia almost but not entirely to the exclusion of the plurilocular. The pool inhabiting Pylaiella has a season extending from October to about June or at latest July.

(b) Lithophytic Pylaiella.

Like the P. rupincola of Kylin these plants are found closely adjoining one another and together form very obvious

patches of vegetation on rock surfaces. As in this species too, the individuals are almost always found bearing unilocular sporangia alone. In winter, from November to February, all examined plants were found to produce these exclusively and from March onward, throughout the summer, the proportion of plurilocular sporangia (nearly always associated on the same plant with the unilocular) increases until in July they comprise about one third of the total reproductive capacity of any plant. Unlike P. rupincola, however, some individuals were observed to bear plurilocular reproductive structures only. These were the gametophytes, which appeared in early spring, during the month of February, and persisted until early summer. Such plants grew at M.H.W.N.T., which is at the upper limit of the distribution, and were very much smaller in size than the typical specimens.

In addition, they usually bore the plurilocular structures terminally on the branches while those borne on the epiphytic and larger permanent lithophytic plants were always intercalary. It seems likely that these plants could be found at all levels in the distribution of lithophytic Pylaiella but because of their small size are overwhelmed by the larger permanent growth. Certainly they were only seen clearly where the vegetation thinned i.e. at the upper limit of the community. (Figs. 20, 21).

3. Life Cycle from Culture Experiments.

(a) Media.

The Erd-Schreiber culture medium was used for all experiments. This is prepared from Büchner and Befkefeld filtered sea water with addition of soil extract, sodium nitrate and disodium hydrogen phosphate. The solution as prescribed proved adequate for the growth of Pylaiella but by doubling the recommended amount of added phosphate and nitrate growth was faster and fertility greatly increased.

The ASP_2 medium of Provasoli (1954) was also prepared. This complex solution is made up from distilled water and four groups of compounds, salts, trace elements, vitamins and "additional nutrients". The medium was prepared as directed and in addition three variations were made with the salt content constant but with the other groups of constituents increased in turn.

All four preparations were found to be unsuitable for Pylaiella, due probably to fluctuation in pH. Erd-Schreiber was therefore used exclusively.

(b) Apparatus.

All actively growing cultures were kept under controlled conditions. These consisted usually of continuous fluorescent lighting from a singe "warm white" strip and a constant

temperature of 10°C. The layout of the apparatus is represented in Fig. 1 . The cooling unit was placed in fresh water and was found to be accurate to 1°C. The dishes merely rested on a metal grid suspended near the surface of the water which received just sufficient agitation for efficient mixing.

Under these conditions the Pylaiella grew well.

(c) Material.

All culture experiments were set up using the zoospores from unilocular sporangia and the plant material employed was both epiphytic and lithophytic. The Pylaiella was collected at low tide and at the time of normal inundation by the sea was placed in clean, cold sea water in a petri dish. This treatment normally induced the rupture of the sporangial wall and release of zoospores. The zoospores were usually released in greatest quantity at neap tides, though the above treatment was found effective for most times and conditions. After release the spores remain motionless for a short time but soon begin to swim about in all directions. They remain motile for not more than fifteen minutes, then either settle down or float to the surface, withdrawing their flagella in each case. About one third of the zoospores do not settle on the substratum but float to the surface coalescing as they do so to form little rafts of cells which are a common sight in any

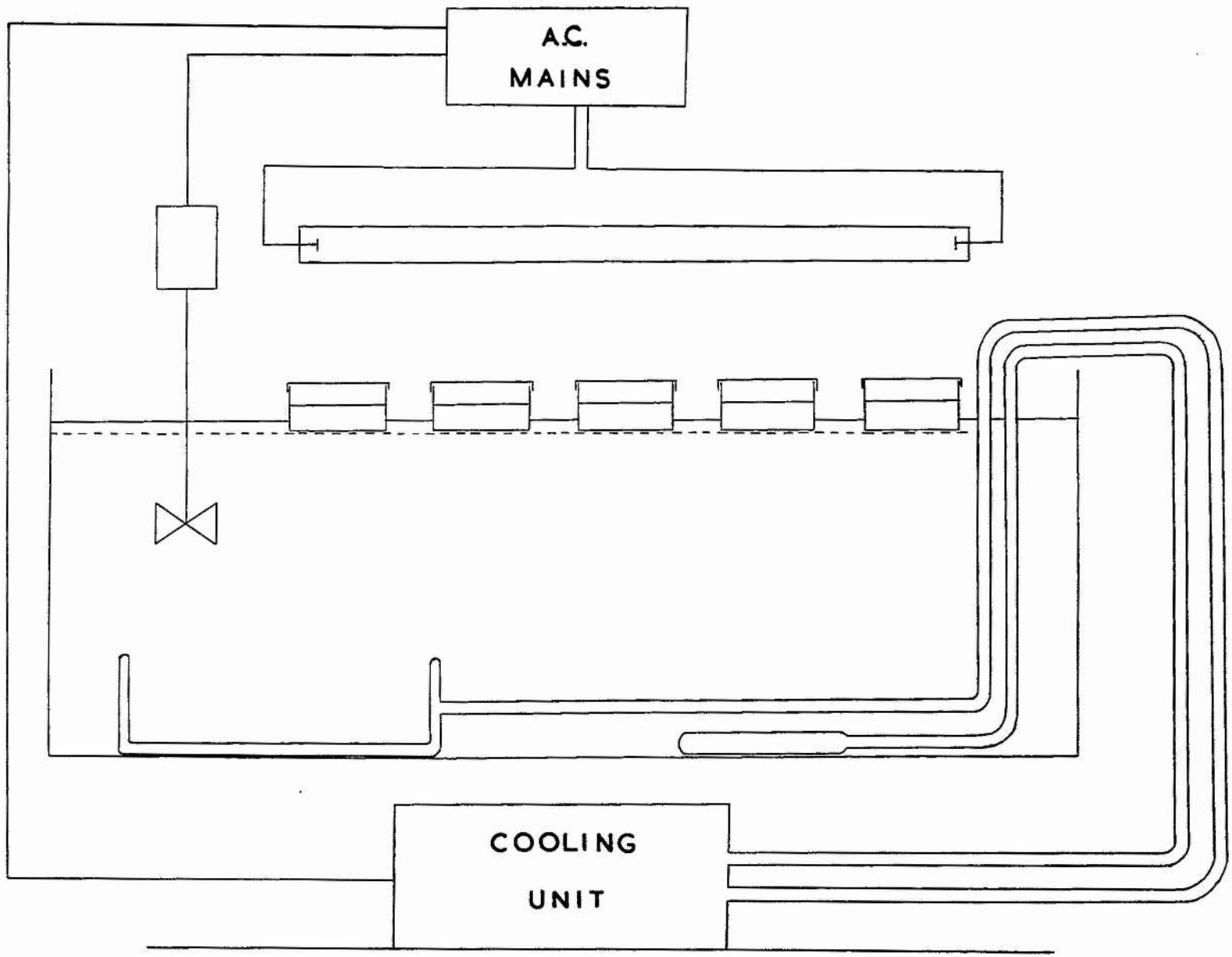


Fig 1

Pylaiella culture. The zoospores were usually pipetted from the examination dish when at the motile stage and transferred to deep sterilised petri dishes containing the culture solution

(d) **Results.**

In all cases the zoospores released from unilocular sporangia of lithophytic plants showed no sigh of fusion and germinated easily and prolifically in culture. The plants grew well and produced, on every occasion, plurilocular gametangia only. These were rarely intercalary in position but were borne terminally either on short lateral branches of long erect filaments or on short erect filaments protruding from the tangle of prostrate growth. The plurilocular gametangia showed a distinct tendency to remain undehisced and most attempts to stimulate release failed. (Figs.22, 23)

On one occasion, however, the plurilocular gametangia were observed to dehisce and the motile zooids were seen to fuse. Kylin (1937) has pointed out the reluctance by the zygotes to grow to maturity. This may also be the case in St. Andrews where the cycle could never be quite completed in culture.

The same behaviour was regularly observed with the epiphytic plants. There was, however, a notable exception. On one occasion zoospores released from unilocular sporangia

were observed to produce a generation again bearing unilocular sporangia. These could not be induced to release zoospores and the culture eventually died.

4. Cytology.

Only Knight and Damman have investigated the cytology of P. littoralis and both have arrived at different chromosome numbers (Knight 2n = 18-20, Damman 2n = 24). Moreover only Damman makes any reference to the techniques employed although from the illustrations it is clear that Knight also used microtomy and cut very thin sections.

All attempts to classify the cytology of the species at St. Andrews were carried out on lithophytic plants (because of their non seasonal distribution and rich production of unilocular sporangia) and all failed.

According to both workers nuclear division takes place when the plants are covered by an incoming tide, and in greatest profusion when this coincides with darkness. Pylaiella was removed regularly from the rocks at all times of the year at both spring and neap tides and in conditions of daylight and total darkness. They were taken to the laboratory where they were plunged into sea water (running or static) at the time when the incoming tide would normally overrun them. They were kept in this sea water during the total period for which they would normally be immersed (i.e. si

hours) and in successive experiments were submitted to varied conditions of temperature and light. Material was also fixed during periods of low tide when the species is uncovered. In all these experiments the material was fixed initially at hourly intervals, later at half hour hour intervals and ultimately every twenty minutes.

(a) Fixation.

The best fixative was found to be weak chrome-acetic acid solution [Johansen (1940)] made up with filtered sea water, and the time for adequate fixation 24-48 hours. The material was then washed in running sea water for 24 hours to remove all chromic acid. This rather lengthy process is the chief disadvantage of the fixative and when rapid fixation was required a mixture of 95% ethyl alcohol and glacial acetic acid in the proportions of three to one, was used.

(b) Staining Techniques.

1. Squashes. Early attempts in cytology were based on the assumption that a squash technique could be devised. This was not possible without premaceration of the tissues and premaceration proved very difficult. Hydrolysation by various acids at different temperatures and strengths had no effect, as had the cytase from the filtered gastric juices of the edible snail Helix pomatia [Fabergé (1946)]. Treatment with sodium carbonate in 6% aqueous solution as used by Naylor (1957) for the Fucaceae proved the most efficient macerating medium, but was still not satisfactory.

Squash techniques were then abandonned in favour of microtomy.

2. Microtomy. The best wax was found to be ordinary paraffin wax with a melting point of 54-56°C. and for optimum clarity of detail in the sections, the blocks were cut at 3μ. Heidenhain's Iron Haematoxylin was the stain most frequently employed (Johansen, 1940) sometimes with Orange G as a counter-stain. Crystal Violet, aceto-carmine, and acetic-orcein and Feulgen were not so satisfactory.

(c) Results

None of the combinations of treatments induced the Pylaiella to a state of clear nuclear division. Resting nuclei were abundant and clear in every preparation. In a few unilocular sporangia mother cells, in certain preparations, the nuclei were observed in a much enlarged condition with a reduced or absent nucleolus and with the chromatin concentrated into very small grains. This presumably constitutes an early stage in division and the chromatin grains are very likely chromosomes, but the number was never clear enough to be counted with accuracy (Fig. 24).

This condition corresponds almost exactly with that depicted in Knight's fig. 22 which she calls "the post synapsis stage". Certainly, too, the number of chromosomes in the sporangia mother cells is small, probably nearer Knight's 9 or 10 than Damman's 12. These facts, while they do not constitute evidence of any worth, would tend to suggest that

reduction division, at least in most cases, does take place in the development of the unilocular sporangia.

5. Deduced Life Cycle for P. littoralis at St. Andrews.

In lithophytic Pylaiella most plants are sporophytes reproducing themselves by means of accessory plurilocular sporangia in summer and in turn producing a population of small haploid gametophytes in spring. The latter bear plurilocular gametangia only and gametic fusion results in more diploid plants for the permanent sporophyte population.

In epiphytic Pylaiella the same sort of cycle probably occurs, with a large population of summer sporophytes reproducing themselves by means of plurilocular sporangia. In winter when found chiefly in pools, these plants bear unilocular sporangia predominantly and their sporangia release haploid zoospores which presumably set up a temporary population (perhaps lithophytic) of small gametophytes.

The case in culture where zoospores released from unilocular sporangia gave rise to a population bearing the same sporangia is probably exceptional, but is probably found equally among epiphytic and lithophytic plants alike. Since no semblance of fusion was ever seen between zoospores it seems best to adopt for this Kylin's explanation for P. rupincola, viz., inhibition of meiosis.

The very obvious predominance of sporophyte individuals

DEDUCED LIFE CYCLE FOR PYLAIELLA LITTORALIS AT ST. ANDREWS.

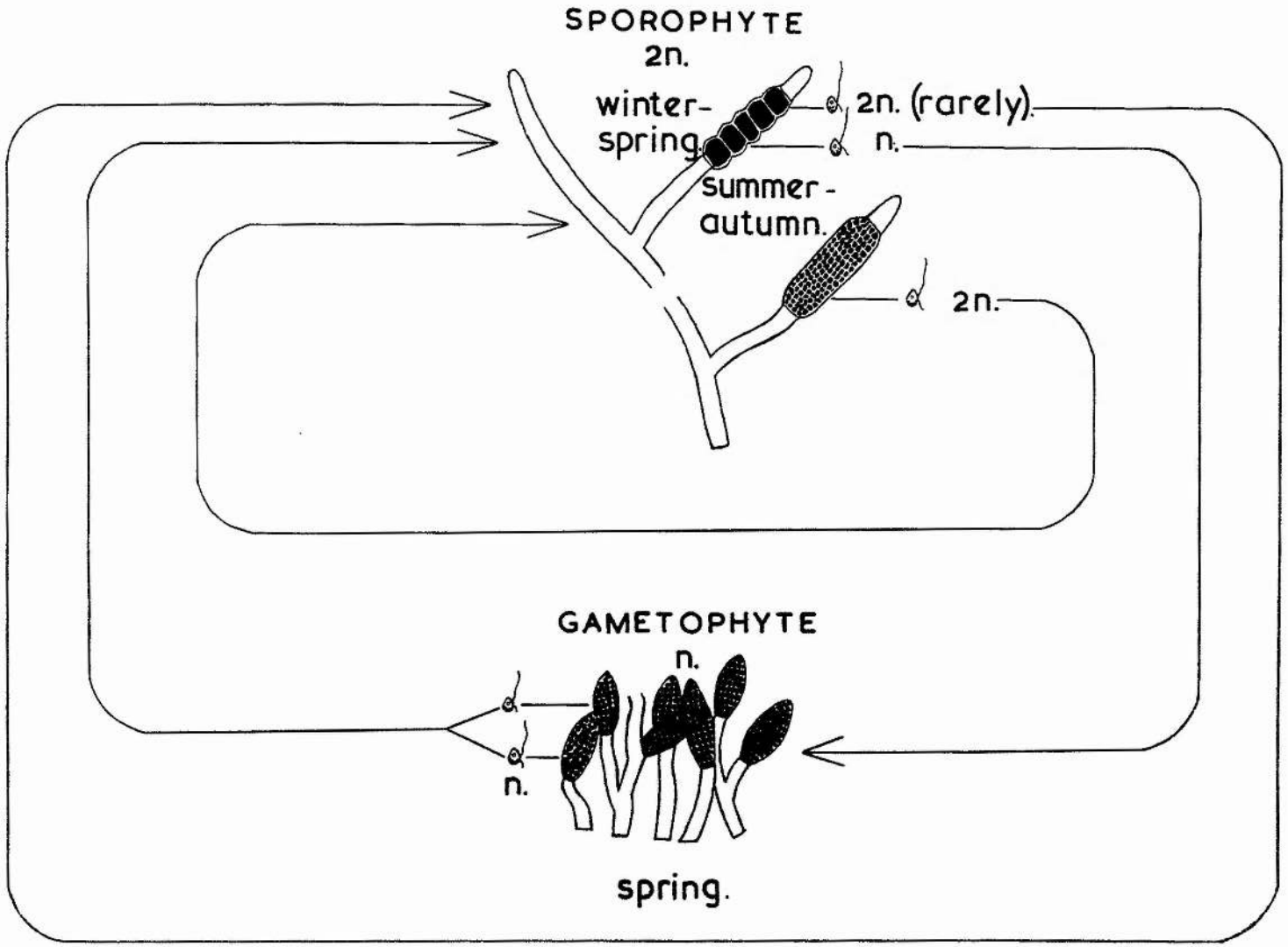


Fig 2

in the Pylaiella population at St. Andrews can be explained by three facts.

(i) The gametophytes are very small in size, the average "frond" length being about 2 mm. and so very easily escape notice.

(ii) From the observed behaviour of zoospores it is evident that a very large number, probably at least 30%, do not settle on a substratum but withdraw their flagella and cease to be motile while still in suspension. This must result in immense loss of numbers. It is perhaps significant that the only Pylaiella gametophytes found in the field have been lithophytic and close to that section of the population which is both permanent in its distribution and richest in its production of unilocular sporangia. Furthermore, they follow upon the season in which the total fertility of the sporophytes has been expressed in unilocular sporangia.

(iii) Their greater fertility coupled with the calmer environmental conditions of summer allows the sporophyte populati to reproduce itself rapidly at this time and so maintain its dominance.

The schematic representation of the life cycle of P. littoralis at St. Andrews is drawn in Fig. 2 .

V. EARLY DEVELOPMENT OF P. LITTORALIS

The development of young Pylaiella was studied only in

plants grown from zoospores. Knight (1923) has described this briefly as has Kylin (1933) who also provides several illustrations. Their observations do not differ materially either from one another or from those made at St. Andrews.

Zoospores are released en masse from unilocular sporangia and remain clumped together and motionless for a period of about ten to fifteen seconds. After this the outer most individuals in each group begin to jerk backwards and forwards, eventually disengaging themselves and swimming off in an erratic fashion. Motility persists for about fifteen minutes, the actual period of motility, as Knight suggests, probably depends on the volume of surrounding medium. In this investigation, most examinations were carried out in small petri dishes, which might explain the brevity of the period.

The zoospores are more or less pyriform with a length of 5-6 μ and an average maximum girth of 3-4 μ. When stained with Heidenhain's haematoxylin it can be seen that the broad end contains 2-3 chromatophores which in some preparations can be seen associated with one or two pyrenoids. A fairly prominent nucleus occupies the central portion and an eye spot can sometimes be distinguished on one side a little nearer the tip. The tip of a zoospore is usually colourless but sometimes contains some granular material. Motility is produced by the longer of the two flagella which are borne laterally in a position about two thirds of the distance from posterior end

to tip. Viewed with dark background illumination the longer flagellum can be seen to be up to about 10μ in length and pointing in a forward direction, the other is about 2-3μ in length and points backwards. (Fig. 25).

When motility ceases, about two thirds of a swarm of zoospores will be found settled on the substratum. This is brought about by applying the flagella bearing part to the substratum. The zoospores then seem to withdraw the flagella and become rounded in shape. It is, however, with that third of the swarm which loses motility while suspended in the medium that the process can be seen most clearly. Zoospores nearing the end of the period of motility tend not to rebound from one another on collision, but remain together. These are joined by many others forming little rafts of cells which rise to the surface. A motile zoospore on approaching one of these rafts inserts the long flagellum between the sides of neighbouring zoospores and by lashing the flagellum backwards and forwards pulls itself into close contact with its neighbours. It then rounds off and forms a cell wall. It should be emphasised that this behaviour is quite different from that shown by fusing gametes and this coalescence of zoospores is not a clump fusion.

Germination takes place after twenty-four hours, as a rule, and is accomplished by the growing out of a long colourless tube from the spore. Nuclear and chromatophore division

presumably takes place and cross walls are quickly formed producing a short filament which creeps over the surface of the substratum. The cells of these prostrate filaments are long and very narrow and contain very few chromatophores. Up to about one week from germination growth in all sporelings keeps apace, and after this varies enormously from individual to individual. One week after germination, the prostrate filament consists of seven to ten cells and at the proximal end a short erect filament can usually be seen. This is much more robust in structure than the prostrate filaments and contains more chromatophores. At this time too the proximal end of the prostrate system begins to branch and spread in all directions over the substratum.

After two weeks a well developed plant will show much branching of the prostrate system which now bears several erect shoots, the shorter and younger specimens being produced from the distal and younger creeping filaments. After three weeks the erect filaments are usually branched and 2-3 mm. in length and in a good culture they may be fertile at the end of one month, but the average time taken for fertility to be reached is about six weeks. (Figs.26,27,28,29)

When the plant has produced a good number of erect filaments and these have reached a length of about 0.5 cm., cable rolling begins to take place. It is not known precisely how this occurs but it seems that the direction of the twining

is chiefly in a clockwise direction which implies that it is a basic attribute of the plant. At any rate the theory that cable strand development is brought about by wave action is clearly untrue for it forms regularly in totally undisturbed cultures.

VI. THE DISTRIBUTION OF P. LITTORALIS AT ST. ANDREWS.

The distribution of Pylaiella littoralis in the St. Andrews area is fairly widespread and its habitats vary accordingly. As these are frequently subjected to diverse environmental conditions the Pylaiella can be found as a component part of several characteristic and different communities. It is, therefore, convenient to explain its distribution by describing the communities separately. The associated differences in form, together with the taxonomic implications, will be discussed later. The more important environmental conditions are described, and where possible measured, for each community.

1. Lithophytic community.

(a) Description.

Although Pylaiella growing directly on rocks and stones seems to be a rather rare feature in most British investigations, it forms one of the most striking and distinctive parts of the St. Andrews distribution and has already been recorded by Dunn (1939).

The herbarium of Batters in the British Museum contains a sheet of Pylaiella specimens collected from Berwick-on-Tweed in January 1887. These are described as rock inhabiting plants, and seem identical with the St. Andrews specimens. Rees (1935) described various algal communities on the shore of Lough Ine, Ireland. There Pylaiella does not occur as a part of any "open shore association", but features in a sheltered littoral "association of sandy and mud covered rocks" in which no species emerge as dominant. From his species list, this community would seem to correspond approximately with the St. Andrews ones. Gibb (1939) examined the marine algal flora of the Great Cumbrae in the Firth of Clyde and recorded Pylaiella in a Rhodochorton rothii community. This occurred on flat or gently sloping rocks found among the sandy beaches of the area, and from the species list would again seem close to the St. Andrews records.

Knight (1923), on the other hand, describes an entirely different distribution. Her work carried out further south on the Isle of Man showed the P. littoralis distribution to be almost solely epiphytic. In only a few cases where the epiphytic Pylaiella was growing extra luxuriantly did she record it spreading to surrounding rock and stones. From her observations she concluded that Pylaiella's relationship with its host plants was one of selective epiphytism approaching parasitism.

Workers in other parts of the world, however, have referred frequently to the species as a lithophytic one and it would appear that this must be a feature of northern waters. Foslie (1890, 1891) has recorded such a growth in Norway, as have Børgesen (1908) for the Faeroes, Setchell and Gardner (1925) for Pacific North America, Damman (1932) for Heligoland, Kylin (1933) for Sweden and Taylor (1957) for the North East Coasts of North America.

The rock on which the Pylaiella grows at St. Andrews is calciferous sandstone and this is found in two conditions. At the south-east of the town, where the coastline runs approximately in an easterly direction to Kinkell Ness, the sandstone is baked and rather hard. In addition it is much folded and this has resulted in a very jagged terrain with many small pools and sandy bays.

Due east of the town and separated from this by about half a mile of beach, the shore again becomes rocky but the stone is quite different in character and formation. It now takes the form of ridges about two to three hundred yards long which project into the North Sea in an approximately easterly direction, separated by strips of sand or boulders. These ridges have a more or less constant dip so that each has a nearly perpendicular northern face, a flat top usually cut longitudinally by a series of pools, and a southern side which slopes gently at an angle of about 20° (Fig.3). In character too this sandstone differs considerably from the other. It/

is extremely soft and crumbly and only in a few isolated patches where a rich concentration of iron deposit occurs does it compare in hardness with the south-east formation.

It is upon the ridges and more especially upon the gentle south facing slopes that the optimum development of lithophytic Pylaiella is found (Fig. 3)

The bulk of the population occurs from 40 cm. below mean tide level almost up to M.H.W.N.T. Nevertheless the distribution shows considerable seasonal fluctuation reaching a maximum in June and July and a minimum in January. This contraction and expansion of the population occurs both upwards and downwards on the sandstone ridges. In late January and February young plants can be found at high water of neap tides and these persist until May or June when they begin to die off, but by June the lower limit of the population has moved down almost to the beginning of the Laminaria zone. In August these low level plants become scarce and by September the population has contracted almost to the winter limits.

The lithophytic plants have a characteristic habit. They are usually rather small, the average length of frond being 1.8 cm. while the longest measured during the investigation was only 4.8 cm. They have a somewhat stunted appearance due to the prominence of the well develpped cable rolling and are dark chocolate brown when damp, lightening to a dark tan when dry. The close proximity of the Pylaiella plants in this

community with one another results in a very noticeable mat of vegetation which in June or July is almost a pure stand interrupted only by plants of Fucus vesiculosus. (Fig.30)

Along with the regular fluctuations in distribution and size, there is also a distinct seasonal variation in the types of sporangia borne by the Pylaiella. Plurilocular sporangia can be found at most times of the year but are scarce during the winter months and almost absent in November and December. At the end of January and in February the small gametophytes can be found at the uppermost limits of the lithophytic distribution. In March some of the plants that form the bulk of the population produce a few plurilocular sporangia among the masses of unilocular sporangia which are always present and in July about one third of the sporangia produced by these plants are plurilocular. In September and October they become much reduced in number leaving only the unilocular sporangia which are formed in profusion throughout the winter months and occur in chains of up to twenty-five in number. Thus the majority of the lithophytic population is sporophytic (probably about 90%) reproducing itself by accessory plurilocular sporangia in summer and the gametophyte in early spring. The high fertility of the lithophytic plants presumably has a contributory effect on their short frond lengths.

The community in which lithophytic Pylaiella grows is

mostly a perennial or pseudo-perennial one but at the same time its members show considerable seasonal fluctuation in numbers and distribution. Fucus vesiculosus is the species most commonly associated with Pylaiella and like it can be found at all times of the year. In summer the two species are co-dominant over a population of Chlorophyta such as Enteromorpha compressa, E. prolifera, Ulva lactuca, Cladophora rupestris and most especially Rhizoclonium implexum, together with some Phaeophyta notably Ralfsia verrucosa and Sphacelaria britannica, and some Rhodophyta, such as Ceramium rubrum, Rhodochorton rothii, and Lithothamnion lenormandii. In winter, the contraction in the Pylaiella population is accompanied by an alteration in appearance of the community. The Fucus vesiculosus becomes the sole dominant, the Pylaiella vegetation having been broken up into small clumps and the luxuriant summer growth of Chlorophyta drastically reduced, while the Ralfsia verrucosa and various members of the Rhodophyta are at optimum development.

When lithophytic Pylaiella is at the uppermost limit of its distribution which is in the spring, the following are the chief associated species.

Chlorophyta.

Protococcus marinus Kütz (as illustrated in Newton, 1931).

Enteromorpha ramulosa (Sm.) Hook

Enteromorpha prolifera (Müll.) J.Ag.

Enteromorpha compressa (L.) Grev.

Chlorophyta (cont.)

Rhizoclonium implexum (Dillw.) Kütz

Rhizoclonium riparium (Roth.) Harv.

Cladophora rupestris (L.) Kütz.

Chaetomorpha aerea (Dillw.) Kütz

Phaeophyta.

Ralfsia verrucosa (Aresch.) J.Ag.

Sphacelaria britannica Sauv.

Ascophyllum nodosum (L.) Le Jol.

Fucus spiralis L.

Rhodophyta.

Bangia fuscopurpurea (Dillw.) Lyngb.

Rhodochorton rothii Naeg.

Ceramium rubrum (Huds.) Ag.

Plumaria elegans (Bonnem.) Schm.

Catenella repens (Lightf.) Batt.

Polysiphonia lanosa (L.) Tandy

Cyanophyta.

Entophysalis crustacea (Ag.) Dr. et Daily

Calothrix consociata (Kütz) B. et F.

Rivularia atra Roth. ex B. et F.

Chrysophyta

Apistonema pyrenigerum Pascher.

Bacillariophyceae.

Many diatoms were found associated with the Pylaiella, the commonest being species of Navicula either free living or in the schizonema condition but species of Licmophora, Grammatophora, Cocconeis and Melosira were also fairly frequent.

The zone from a little below mean tide level to a little below mean high water of neap ties is that which contains the greatest concentration of Pylaiella and the following species are commonly found. The seasons of their greatest frequency are indicated.

Chlorophyta.

Monostroma grevillei (Thur.) Wittr. - Summer (almost absent in winter)
Ulva lactuca L. - Summer
Enteromorpha compressa (L.) Grev. - Summer
Enteromorpha linza (L.) J.Ag. - Summer
Enteromorpha prolifera (Müll) J.Ag. - Summer
Enteromorpha ramulosa (Sm.) Hook. - Spring (not recorded at other seasons)
Cladophora rupestris (L.) Kütz. - All year
Rhizoclonium implexum (Dillw.) Kütz. - Summer
Chaetomorpha aerea (Dillw.) Kütz. - Spring
Spongomorpha lanosa (Roth.) Kütz. - Summer
Rhizoclonium riparium (Roth.) Harv. - Summer

Chlorophyta (cont.)

Prasiola stipitata Suhr. - Autumn, Winter and Spring.

Prasiola crispa (Lightf.) Menegh. - Autumn, Winter and Spring.

Phaeophyta

Ralfsia verrucosa (Aresch.) J.Hg. - Autumn, Winter.

Leathesia difformis (L.) Aresch. - Summer

Sphacelaria britannica Sauv. - All year.

Sphacelaria radicans (Dillw.) Ag. - Winter, Spring.

Laminaria digitata (Huds.) Lamour - All year

Laminaria saccharina (L.) Lamour - All year

Ascophyllum nodosum (L.) Le Jol - All year

Fucus serratus L. - All year

Fucus spiralis L. - All year

Fucus vesiculosus L. - All year

Pelvetia canaliculata (L.)Dene. et Thur. - All year

Rhodophyta

Rhodochorton floridulum Naeg. - All year but scarcest in summer.

Rhodochorton rothii Naeg. - All year but scarcest in summer.

Chondrus crispus (L.)Stackh. - All year

Gigartina stellata (Stackh.) Batt. - All year

Corallina officinalis L. - All year

Lithothamnion colliculosum Fosl. - Autumn, Winter & Sprin

Lithothamnion lenormandii (Aresch.) Fosl. - Autumn, Winter & Sprin

KEY TO SPECIES

E	Enteromorpha compressa (L.) Grev.	G	Gigartina stellata (Stackh.) Batt.
U	Ulva lactuca L.	Ll	Lithothamnion lenormandii (Aresch.) Fosl.
R	Ralfsia verrucosa (Aresch.) J. Ag.	La	Lomentaria articulata (Huds.) Lyngb.
Fs	Fucus serratus L.	C	Ceramium rubrum (Huds.) Ag.
Fv	Fucus vesiculosus L.	Pe	Plumaria elegans (Bonnem.) Schm.
Rr	Rhodochorton rothii Naeg.	Lp	Laurencia pinnatifida (Huds.) Lamour.

P Pylaiella littoralis (L.) Kjellm.

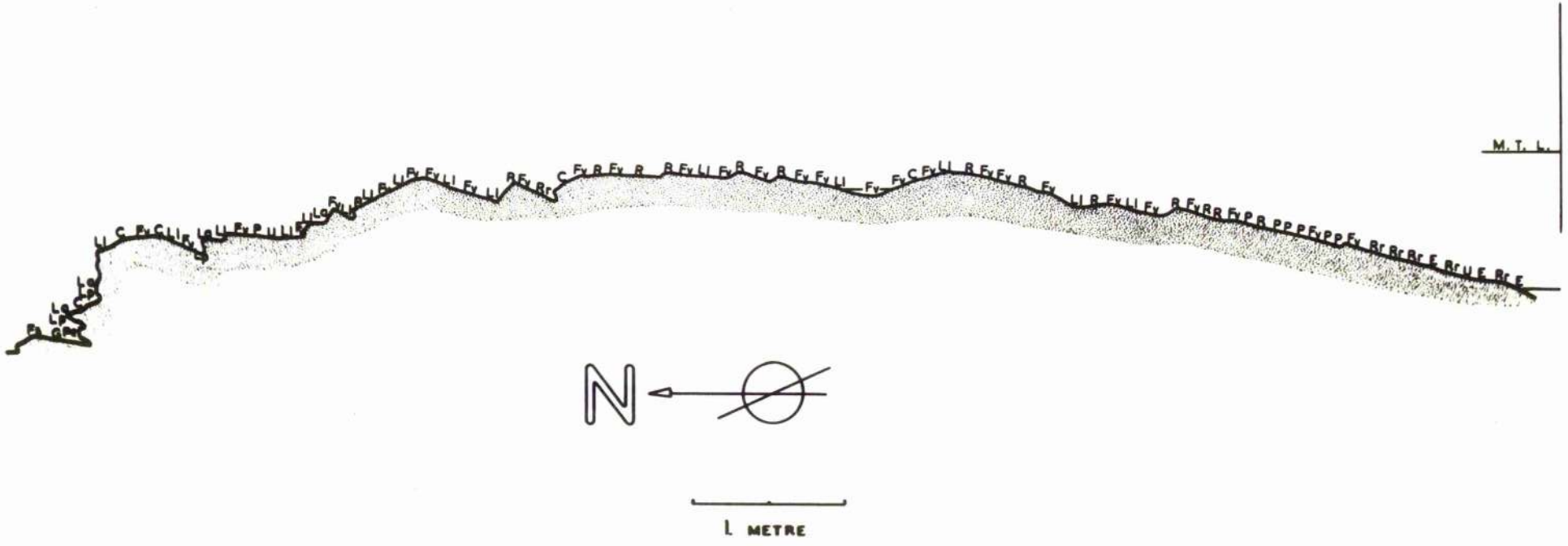


Fig.3

Rhodophyta (cont.)

Lomentaria articulata (Huds.) Lyngb.	- Autumn, Winter & Spring
Plumaria elegans (Bonnem.) Schm.	- Autumn, Winter, & Spring
Membranoptera alata (Huds.) Stackh.	- Autumn, Winter & Spring.
Laurencia pinnatifida (Huds.) Lamour	- Autumn, Winter & Spring
Polysiphonia lanosa (L.) Tandy	- All year
Polysiphonia nigrescens (Sm.) Grev.	- Autumn, Winter & Spring.

Cyanophyta

Rivularia atra Roth. ex B. et F.	- Autumn, Winter and sprin

Chrysophyta and Bacillariophyceae are as given for the high level zone.

The distribution of these species within the zone of Pylaiella growth is typical. Damp crannies and shaded north facing ledges accommodate the heliophobic members of the Rhodophyta while the Pylaiella is more common on the sunny south facing slopes along with Fucus vesiculosus and some members of the Chlorophyta. This feature is best seen in the transect (Fig. 3) of a typical sandstone ridge. The transect covers the upper part of the ridge only but it shows the steeply sloping north face, the somewhat eroded top and the beginning of the gentle south slope. The distribution of algae is shown for the month of January.

During July and to a lesser extent in June and August, Pylaiella extends its range almost to low water of neap tides

where its most common associates are Ulva lactuca, Fucus serratus, Laminaria saccharina, Laminaria digitata, Corallina officinalis, Chondrus crispus, Lithothamnion lenormandii, Gigartina stellata, Ceramium rubrum and Rhodochorton rothii.

(b) Environmental Factors.

(i) Wave Action. The direction of wave action is usually from the north-east and most of the Pylaiella growth is therefore on the leeward slopes of the ridges. Nevertheless the effect of any storm is to remove large numbers of the erect tufts and this is most marked in the late summer and autumn when early gales cause the disappearance of the largest plants.

(ii) Substratum. This factor is closely related with the former. To an algal population the physical nature of the rock on which it grows is of greater importance than its history. The calciferous sandstone which forms the substratum for Pylaiella is extremely soft and wave action of even moderate force is often sufficient to break off large pieces of the rock (Fig. 31). These pieces, frequently bearing masses of Pylaiella, have been observed after removal, and been seen to disintegrate under the pounding of one or two tides.

(iii) Turbidity. Excessive wave action also raises the turbidity of the water. This, apart from impeding light penetration, produces a deposit of silt to which Pylaiella seems especially sensitive. The presence of this silt seems

to encourage the development of a microfauna and flora consisting of flagellates, bacteria etc. whose activities may well inhibit reproduction because plants in this condition, though fertile, could never be induced to release zoospores.

(iv) Light. It can be seen from the level that Pylaiella occupies on the shore that most of its individuals are covered by every tide. On such plants insolation seems to have little effect, beneficial or otherwise. On the brightest summer days, exposed Pylaiella rapidly assumes a very dried up appearance, but close examination shows that only the outermost filaments are in fact dry; those underneath and close to the rock remain damp until covered by the tide. For the gametophytes and other plants of Pylaiella that grow at H.W.N.T. and above, in early spring, the periods of exposure become too long, for by the end of June most have disappeared but as they are not at that time exposed to excessive sunlight the chief effect is one of desiccation. Certainly, it is the increasing light factor in spring and early summer which allows the downward migration of the species on the shore.

(v) Temperature. Closely related to the previous one, this factor seems to have considerable influence on the growth of Pylaiella. The mean lengths of two hundred and fifty tufts of lithophytic Pylaiella taken monthly from the same community, from November 1957 until October, 1958, are arranged in the graph (Fig. 4) and the range of the individual monthly

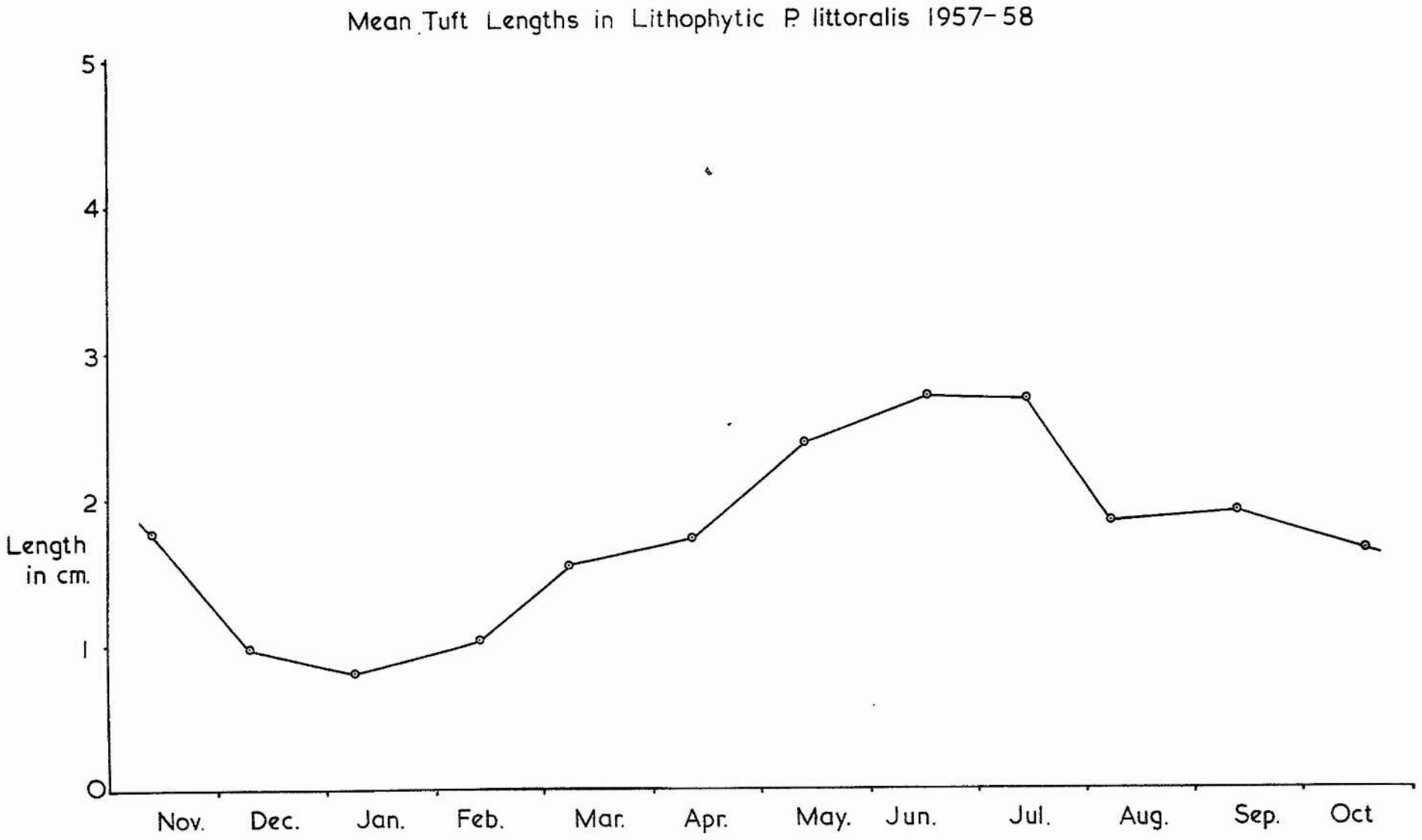

Mean Tuft Lengths in Lithophytic P. littoralis 1957-58
Length in cm.
5
4
3
2
1
0
Nov.
Dec.
Jan.
Feb.
Mar.
Apr.
May.
Jun.
Jul.
Aug.
Sep.
Oct

Fig. 4

Tuft Lengths in Lithophytic P. littoralis

Monthly Samples of 250 Tufts

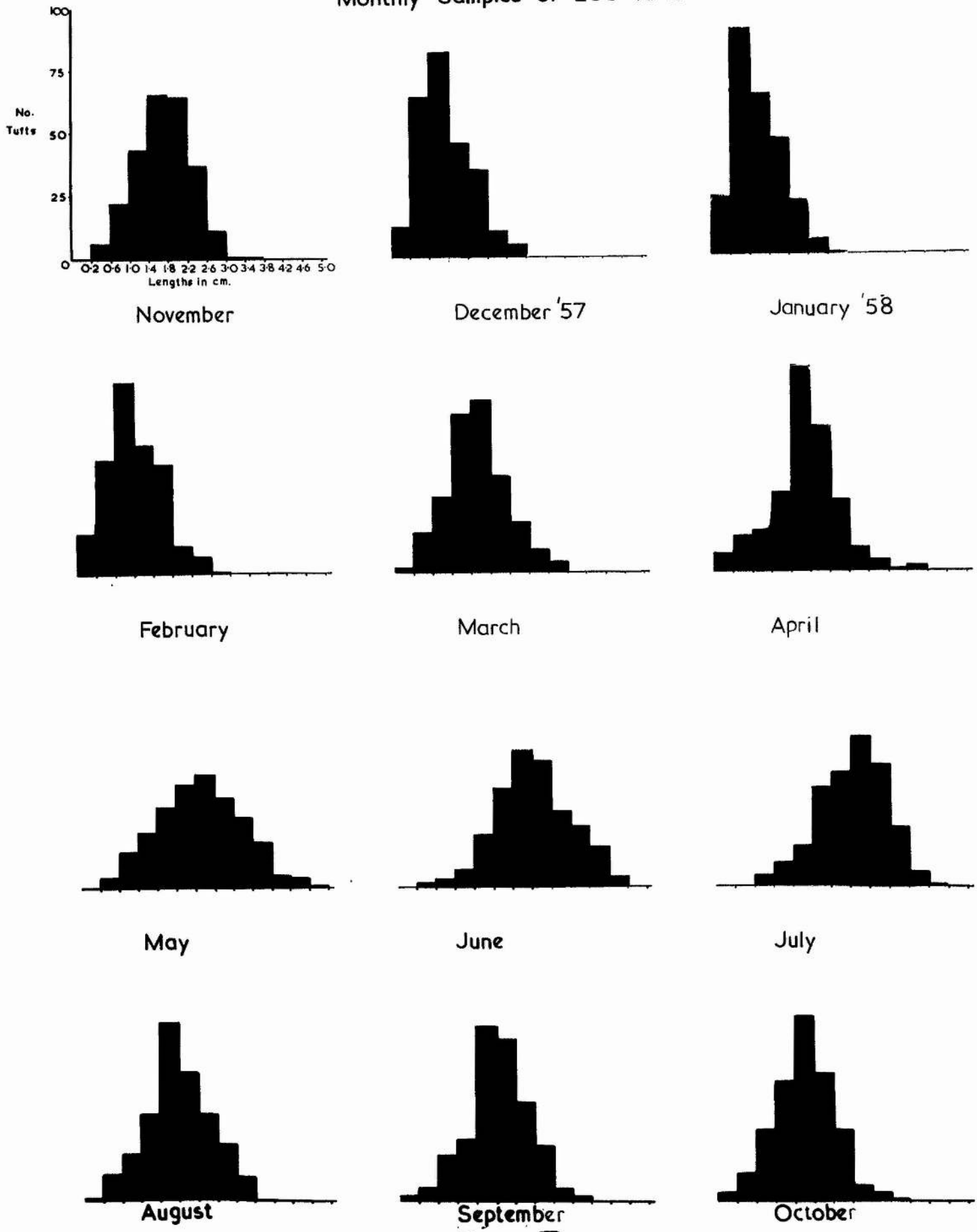
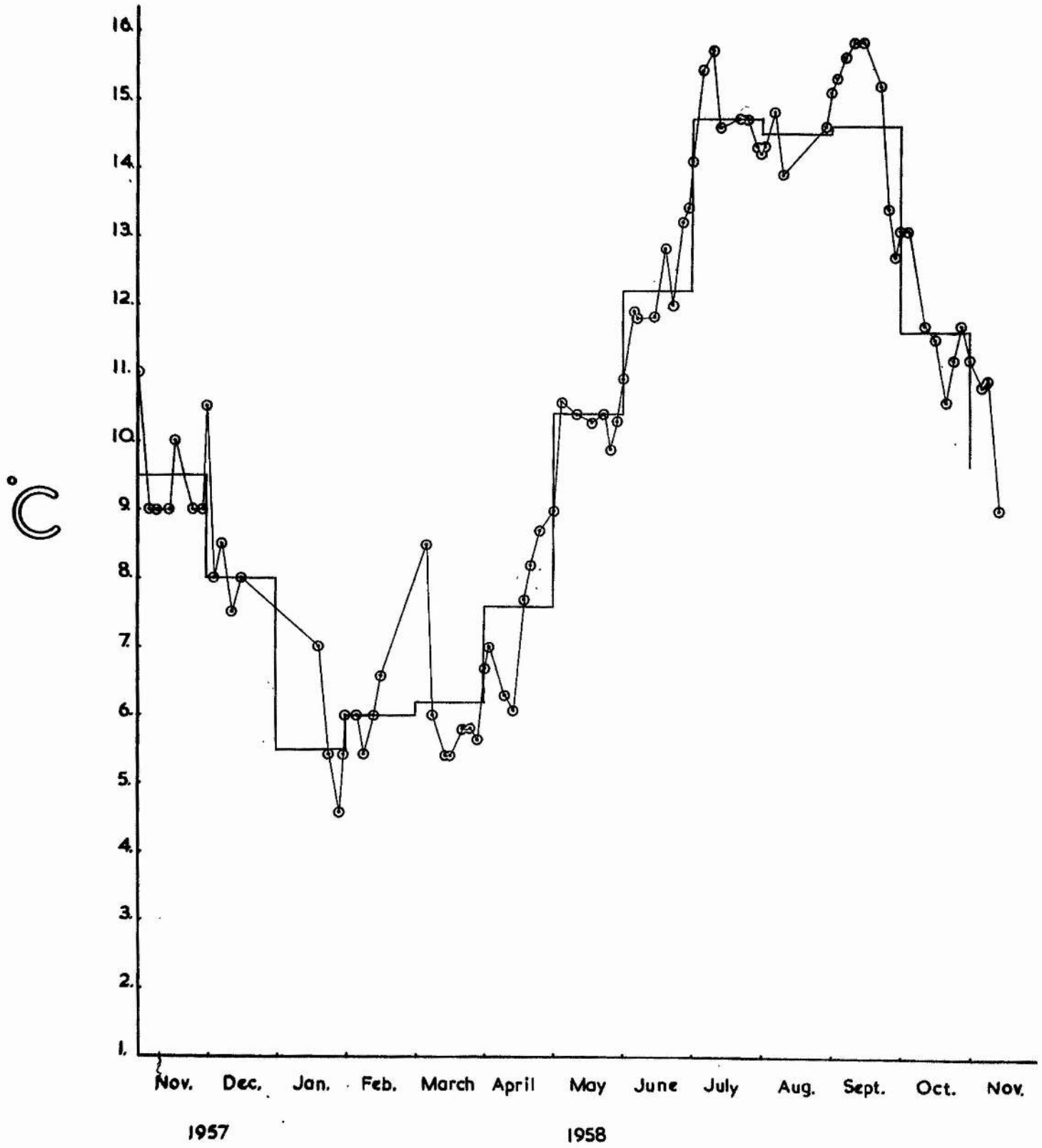


Fig. 5



Individual and Monthly Mean Temperatures of Inshore Sea Water

1957–58.

Fig. 6

measurements illustrated by the histograms (Fig. 5). These show an extremely close similarity to the fluctuations in temperature of inshore sea water for the same period (Fig. 6). Sea temperature information for St. Andrews comes from the Bell Rock lighthouse, but as this is some 14½ miles from the coast it cannot give a true picture of the shore temperatures, and inshore sea water, in fact, follows the fluctuations in air temperature fairly closely. It is of interest to note that the slight increase in mean length of the Pylaiella in September 1958 over that of the previous month is paralleled by a similar increase in the sea temperature. The sea temperatures were measured on the water which is pumped continuously into the large fish tanks at the Gatty Marine Laboratory, St. Andrews.

(vi) Dissolved Oxygen. The sea water as it breaks on the rock surfaces is always sufficiently agitated to ensure a high oxygen concentration but the actual oxygen requirements of lithophytic Pylaiella are not known.

(vii) Salinity. The salinity of sea water was measured on several occasions by means of hydrometry and conversion by Knudsen's Hydrographical Tables. This gives fairly accurate results and shows the salinity at St. Andrews to be typical for the North Sea. On one occasion after three days of heavy rain the measured sample had a salinity of 30.68‰, the lowest recorded. The highest recorded salinity was in January 1959

when a figure of 34.14‰ was found. It is of interest to note that a few days after this latter measurement, a sample of off shore plankton contained the Chrysophyte, Halosphaera viridis Schmidt., which is an accepted indicator of Atlantic sea water. The average salinity for inshore sea water at St. Andrews seems to be about 33.50‰ and none of the fluctuations in salinity seems sufficiently drastic to have any effect on the Pylaiella.

(viii) Hydrogen Ion. The pH of sea water was also measured on several occasions by means of a Lovibond Comparator, a simple apparatus making use of coloured indicator dyes. The indicators used were Cresol Red (range 7.2-8.8) and Phenol Red ((6.8-8.4), both manufactured by B.D.H. Measurement of pH in sea water by the normal electrolytic methods raises difficulties in conductivity and is liable to produce inaccuracie For routine measurements the indicator method proved quick and satisfactory. These measurements showed the sea on the coast at St. Andrews to have an average pH of 8.4 with only a small fluctuation which had no observable effect on the Pylaiella.

(c) Flora and Faunistic Notes.

(i) Epiphytes on Lithophytic Pylaiella.

(a) Phormidium fragile Gom. This blue-green alga is always present on the filaments of the Pylaiella and is usually

most common on the tips of branches and on unilocular sporangia. It is sometimes present in large quantity but does not appear to have any adverse effects on the growth and reproduction of the plants. It is the chief epiphyte on lithophytic Pylaiella and seems to be most common in summer.

(b) Diatoms. These are also very common epiphytes and in most cases are of the genera Navicula and Licmophora.

(c) Entocladia viridis Reinke. This is found as a mass of greenish unicells which are closely applied to the filaments. Although a common epiphyte it has never been observed in sufficiently large numbers to interfere with the growth of the plants.

(d) Protococcus marinus Kütz. Found on the Pylaiella at high water mark this is a rare and apparently harmless epiphyte. It is in appearance identical with the illustration of Newton (1931).

Several other species have been observed as epiphytes on lithophytic Pylaiella but all have been in very juvenile conditions, which prevents accurate identification but the most regular records seem to be of species of Enteromorpha and Acrochaetium.

(ii) Occurrence as an Epiphyte.

These plants of Pylaiella are virtually exclusively lithophytic. They will grow in dense mats around plants of

Fucus vesiculosus but have never been observed to migrate from the rock surfaces either on to its thallus or to those of any of the other likely hosts such as Ceramium rubrum and Ascophyllum nodosum.

There are however three exceptions to this, for typical lithophytic Pylaiella has been recorded as an epiphyte on Ralfsia verrucosa, Lithothamnion lenormandii, and Chaetomorpha aerea. Pylaiella occurs quite commonly on the first two species but it should be noted that both are crustose algae which provide a thallus surface not so very different from that of the rock. The instance of Pylaiella growing on Chaetomorpha aerea is not so easily explained but as this has only been observed once and as this is the sole example of Pylaiella from this community growing on an erect host, it can be concluded that as a rule the occurrence is rare.

(iii) Eurychasma dicksonii (Wright) Magnus.

This marine Phycomycete was the only parasitic plant observed on Pylaiella. Its occurrence is widespread and apparently shows little seasonal fluctuation, but it is never very common. It may be found in vegetative cells of all ages but more usually in the younger parts of the plant and also in unilocular sporangia. Fruiting seems most frequent in winter when the round colourless sporangia are sometimes seen protruding from cells and sporangia.

(iv) Recolonisation of Rock Surfaces.

As has been mentioned the substratum of lithophytic Pylaiella is extremely friable and wave damage is extensive. Hatton (1932) is one of the workers who has investigated algal repopulation in the Fucus vesiculosus zone. He observed that in nearly all cases baring of the rock surface was followed by a growth of green algae, usually Enteromorpha compressa, which eventually disappeared when the young Fucus grew to a certain length, this being apparently that of a greater length than the Enteromorpha. Recolonisation within the Pylaiella zone at St. Andrews follows this very closely. There is first a very rapid growth of Enteromorpha (E. prolifera and/or E. compressa) which fruits, dies and springs up again for up to three times. Generally during the growth of the second crop the young Fucus plants appear but these grow slowly and when the Enteromorpha dies down for the last time are only 1.0 to 2.0 centimetres high. After the removal of the Enteromorpha the young Pylaiella appears among the Fucus.

The time taken for complete recolonisation varies according to the season on which the rock was first bared. If bared in winter, the return of Fucus and Pylaiella in the customary proportions takes about eight months, but in summer with rapid growth this may be accomplished in half the time. In all cases the rock was laid bare simply by chiselling off the surface layer.

(v) Fauna.

The animal most commonly associated with this community of Pylaiella is the marine amphipod, Marinogammarus marinus (Leach). This gregarious animal is found at all times of the year and in large numbers among the tufts and erect shoots. Its role in the ecology of Pylaiella is not clear but as its diet is largely vegetarian, the probability is that it grazes fairly heavily on all parts of the fronds. At the same time it almost certainly reduces the numbers of micro-organisms frequently found at the bases of Pylaiella shoots.

A less frequent, but definitely more harmful associate is the larva of the Dipteran fly Clunio marinus Haliday. This animal can also be found at all times of the year but is especially common in the summer months. It is an active vegetarian and feeds extensively on the younger shoots of Pylaiella. Examination of the plants in summer often reveals specimens practically devoid of young branches and consisting of the central cable strand alone. If this is carefully dissected the Clunio larvae are invariably found inside.

An unidentified species of Rhabdostyla (a ciliated Vorticella-like organism) is also common on Pylaiella and is found throughout the year but apart from its removal of a few zoospores cannot affect the distribution to any extent. The same is true for the Nematode worms, Patella vulgata, Mytilus edulis and Balanus balanoides which complete the list of the most common associated animals.

2. Boulder Community.

(a) Description.

North of the town of St. Andrews and running in an east-west direction there is a cliff formation about fifty feet in height. Like the previously described rock, the cliff material is easily eroded and continuous wave actions has resulted in regular falls of rock. The breaking up of these rock falls has produced many large boulders which have been rapidly colonised by various species of algae, including Pylaiella littoralis. (Fig.32).

Although the Pylaiella is again strictly lithophytic the plants differ in certain respects from those previously described Also this community is numerically poorer in species, having a greater development of creeping filamentous algae such as Sphacelaria, Rhodochorton and Rhizoclonium to the exclusion of crustose forms such as Lithothamnion. These facts merit its discussion separately.

The Pylaiella plants are much bigger than those from the main lithophytic community, the average frond length at optimum development being about 10 cm. with a maximum of about 15 cm. The fronds are rather isolated in the community, a quite different condition from that of the closely adjoining lithophytic individuals and in form they lack the prominent cable rolling so characteristic of the latter. Another feature

in which the communities are unalike is that in the boulder community the Pylaiella distribution is strictly seasonal. The first appearance of the species is in March, the maximum development in July and by October most of the plants have disappeared.

Sporangial development by the plants is considerable though not so profuse as in those of the main lithophytic community, and all examined specimens were observed to produce unilocular sporangia alone. One individual examined in September 1958 was found to have a chain of no less than thirty-three unilocular sporangia, the largest number recorded during the investigation for Pylaiella in any community.

When the first young plants of Pylaiella are found in this community, an event which takes place usually in March or April, the chief associated species are Rhodochorton rothii, Sphacelaria radicans, S. britannica, Ceramium rubrum (massed juvenile plants) Ralfsia verrucosa, Cladophora rupestris and Rhizoclonium implexum. Two months later the Chlorophyta begin to become dominant and by July Rhizoclonium is present in large masses accompanied by species of Enteromorpha, Ulva and Cladophora. It is at this stage that the Pylaiella reaches optimum development and the community has the appearance of a tangled confusion of Chlorophyta with many brown streaks indicating the Pylaiella plants and accompanied by red patches of Callithamnion brodiae and Rhodochorton rothii.

As the Pylaiella plants are fairly large and delicate they become easily detached by wave action and autumn storms usually remove most of the population. The removal is not always complete and probably more often than not the rhizoidal portions of the plants remain entangled with the Sphacelaria but their viability and powers of regeneration could not be assessed.

Chief associated species are:-

Chlorophyta

Prasiola stipitata Suhr.

Enteromorpha compressa (L.) Grev.

Enteromorpha linza (L.) J.Ag.

Enteromorpha prolifera (Müll.) J.Ag.

Ulva lactuca L.

Cladophora rupestris (L.) Kütz.

Rhizoclonium implexum (Dillw.) Kütz.

Phaeophyta

Ralfsia verrucosa (Aresch.)J.Ag.

Sphacelaria britannica Sauv.

Sphacelaria radicans (Dillw.) Ag.

Fucus serratus L.

Fucus spiralis L.

Fucus vesiculosus L.

Ascophyllum nodosum (L.) Le Jol.

Rhodophyta.

Bangia fusco-purpurea (Dillw.) Lyngb.

Acrochaetium spp.

Rhodochorton rothii Naeg.

Chondrus crispus (L.) Stackh.

Callithamnion brodiae Harv.

Ceramium rubrum (Huds.) Hg.

Polysiphonia lanosa (L.) Tandy

Polysiphonia nigrescens (Sm.) Grev.

Cyanophyta

Calothrix consociata (Kütz) B. et F.

Microcoleus chthononlastes Thur. ex Gom.

Chrysophyta

Apistonema pyronigerum Pascher.

Bacillariophyceae

As for lithophytic community.

(b) Environmental Factors.

(i) Wave Action. The area in which the boulders lie receives moderate wave action but this is aggravated by the swirling and sucking of the waves as they break on the cliffs and fall back on the next oncoming wave. The destructive effect on the community in general and on the Pylaiella in particular

is considerable and as an ecological factor wave action is very important in this area.

(ii) Light. The boulders lie at the base of a cliff which faces almost due north. The result of this is that for the winter months the entire area is in constant shadow and that even in mid-summer the period of direct sunlight received by it is short. The sudden increase in strength and period of sunlight that the algae experience in April-May seems certainly to trigger off the development of Chlorophyta but less certainly the Pylaiella.

(iii) Temperature. This factor is probably the more important. The sea temperatures and their significance are as for the lithophytic plants.

(iv) Dissolved Organic Substances: This area is one of those in which the tides frequently deposit storm dislodged seaweeds. The decay of this material releases organic compounds which Fischer-Piette (1929) suggested are an ecological factor of some importance. He devised a method for its quantitative measurement and a scale of concentrations but no attempt was made to repeat this at St. Andrews. It is probable, however, that the concentration of these substances here is greater than at the main lithophytic community, but the effect is not evident.

(v) Turbidity. Much of the debris that falls from the cliff top is a fairly fine soil. The sand at the base of the cliff has also a rather small particle size. As a result of the wave action the water is frequently turbid, but the abrasive action while harmful to some species does not seem particularly destructive to the Pylaiella.

The layer of silt that forms on the boulders favours the growth of species such as Sphacelaria britannica, Rhodochorton rothii and Rhizoclonium implexum. It also seems less unfavourable to the Pylaiella here than to that in the lithophytic community. This is most probably because the binding action of the Sphacelaria and Rhodochorton preserves a fairly stable substratum.

(vi) Salinity. There is often a seepage of fresh water from various parts of the cliff face but this is never in great quantity. Also the water that does drop to the base of the cliff is absorbed immediately by the sand and never comes in contact with the Pylaiella which grows at a height of about 50 cms. above the sand.

It is therefore assumed that the Pylaiella is covered by sea water of normal salinity.

(vii) Hydrogen Ion Content. This differs neither in range nor effect from that of the sea water surrounding the lithophytic community.

(viii) Dissolved Oxygen. As for the lithophytic community.

(c) Flora and Faunistic Notes.

(i) Epiphytes. The Pylaiella in this community is remarkably free from epiphytes, the blue-green Phormidium fragile Gom. being found but not in such great profusion as on the truly lithophytic plants. The only other recorded epiphytes are diatoms and these are almost exclusively of the genus Navicula.

(ii) Occurrence as epiphytes. As in the first community the Pylaiella plants again grow on the stone surfaces. Due to the dense tangle of vegetation, however, it is not always easy to distinguish lithophyte from epiphyte, and some individuals undoubtedly occur as epiphytes, but these are exceptional.

(iii) Fauna. The dense growth of creeping filamentous algae such as Sphacelaria, Rhodochorton and Rhizoclonium, and the layer of silt, do not favour such species as Balanus balanoides, Mytilus edulis and Patella vulgata. Marinogammarus marinus is common but not in such great numbers as among the main lithophytic community and the Chironomid larva Clunio marinus Haliday occurs frequently. The latter browses extensively on the Pylaiella and other algae. Probably the commonest animals are Nematode worms, which along with various flagellates and other micro-organisms form the biggest proportion of the fauna associated with this community.

3. Epiphytic Community.

Although the lithophytic mode of growth is an accepted feature of Pylaiella littoralis, especially in northern waters, the species is still regarded as typically epiphytic, and some workers such as Knight (1923) have maintained that the condition is one of selective epiphytism approaching parasitism. At St. Andrews a large proportion of the Pylaiella grows epiphytically and the range of hosts covers some ten species. It is also true that the majority of epiphytic plants at any time of the year are to be found on certain members of the Fucaceae and to this extent the epiphytism is selective. However the fact that close examination of Pylaiella growing on several different hosts has never shown extensive penetration by rhizoidal filaments would suggest that the Pylaiella - host relationship is one of true epiphytism. This is also borne out by a simple experiment in which sporelings of epiphytic Pylaiella were grown in Erd-Schreiber culture medium. This was made up as prescribed and to some of the solution was added a Fucus extract made by macerating healthy adult fronds and filtering the mixture. Some of the sporelings were placed in the ordinary culture medium and some in the enriched, and the subsequent development observed. This showed development to be equally robust in both solutions.

Both Knight (1923) and Kylin (1933), who have investigated the species closely, have observed a link between the type of

sporangia borne by the Pylaiella and the species of host plant. These findings are discussed fully in the section on life cycle but it is repeated here that this host species - sporangium type connection is not obtained at St. Andrews. For example, in summer plurilocular sporangia predominate and most plants of Pylaiella whether growing on Ascophyllum, Cladophora or Fucus bear these, along with a small proportion of the unilocular form, while during the winter the same range of hosts carries plants bearing the unilocular sporangia to the near exclusion of the plurilocular. It would seem probable that for St. Andrews the seasonal differences are most important.

This seasonal variation in the types of sporangia formed by epiphytic Pylaiella is accompanied by a migration of successiv crops up and down the shore to different types of habitat. During summer and early autumn, the plants are large and restricted to hosts growing on open rocky parts of the shore, while in winter and spring the species as an epiphyte occurs chiefly in pools at or near high water of neap tides. It is therefore convenient to describe these phases in its distribution separately.

A. SUMMER-AUTUMN DISTRIBUTION.

(a) Description.

The most common host is undoubtedly Fucus vesiculosus and it is usually also the host on which the Pylaiella first appears. The Pylaiella seems to grow most frequently on F. vesiculosus

at places where an outcrop of rock emerges from the sand, and at low tide the epiphyte is seen as a fan shaped tuft spreading from the branches of its host (Fig.33).

Kylin (1937) mentions that these plants favour the youngest parts of the host thallus. This is generally the case at St. Andrews, but as many of the Pylaiella plants also occur on the lower fronds and stipes, it would seem probable that the apparent "preference" for the younger parts is due merely to the greater area offered for colonisation by the latter. The fact that most specimens of Pylaiella occur on large, fully grown hosts would also seem to bear this out.

The first appearance of epiphytic Pylaiella in this phase of its distribution may be as early as February when the occasional small tuft can be found on Fucus vesiculosus. Development seldom becomes evident, however, until April and the plants are only noticeable in May. In size, the plants are large, the average at maximum development being in the neighbourhood of fifteen to twenty centimetres, while in some localities some were measured with a frond length of thirty centimetres. Maximum size and greatest number of individuals is obtained in July and August. During June, the lower limit of the distribution spreads into the Fucus serratus zone and in July and August plants occur on the stipes of Laminaria digitata. The uppermost part of the Laminaria zone seems to represent the lowest level on the shore favourable to epiphytic Pylaiella.

As Knight (1923) has observed in the Isle of Man, autumn storms cause immense damage to the large epiphytic plants. In some cases the weight of the epiphytes puts so much strain upon the hold fasts of its host plants that even moderate wave action causes the latter to be removed bodily from the substratum. Sometimes, however, the Pylaiella alone is removed. When this happens, a short stunted piece of Pylaiella, usually consisting of two to three centimetres of cable strand may remain attached to the host and may persist in a viable condition until the following year when further growth may be initiated. This event is rather exceptional, however.

During the summer epiphytic Pylaiella is extremely fertile and sporangia are produced in great profusion. Plurilocular sporangia predominate. A brief examination of a mature plant usually gives the impression that it bears plurilocular sporangia alone but close scrutiny usually reveals a few unilocular sporangia associated with them. The latter occur in chains of up to fifteen in number. It is exceptional to find a plant of epiphytic Pylaiella with a majority of unilocular sporangia during the summer.

With regard to the range of host plants, Knight's observations of Fucus vesiculosus, F. serratus, and Ascophyllum nodosum are confirmed though the latter is an uncommon host (see Flora and Faunistic Notes (iii)).

Kylin (1933) and (1937) observed the gametophytes of epiphytic Pylaiella growing on Sertularia (Dynamena) pumila, in turn epiphytic on Ascophyllum nodosum. Dynamena pumila is not common on the Fuci at St. Andrews but Polysiphonia lanosa fills a similar ecological niche. This species, however, was not a common host for Pylaiella.

The majority of summer epiphytic plants are found on F. vesiculosus; F. serratus, F. spiralis and Laminaria digitata are less common hosts, and Ascophyllum nodosum infrequently colonised. A few other species such as Polysiphonia lanosa, Ceramium rubrum, Cladophora rupestris and Enteromorpha compressa have been observed bearing a growth of Pylaiella but in all cases the plants were small and the occurrence rare.

(b) Environmental Factors.

(i) Wave Action. Again this is a most important factor in the distribution of epiphytic Pylaiella in that it carries the spores to the hosts and eventually removes the mature plants. Otherwise no effects were noted.

(ii) Light. This factor determines the level at which the species can grow and doubtless the strength and length of the summer daylight allows it to spread downwards into the Laminaria zone. Prolonged insolation does not seem to harm the plants and desiccation was never observed. This is probably

because the mass of filaments lying side by side set up a strong capillary action and therefore retain a considerable volume of water throughout a period of exposure.

(iii) Temperature. The sea temperatures have already been given and their effect discussed.

(iv) Dissolved Oxygen. The summer epiphytic Pylaiella receives the normal concentration of dissolved oxygen in the open sea.

(v) Salinity. The salinity of the sea at St. Andrews is given under Lithophytic Community and discussed therein.

(vi) Hydrogen Ion. As before.

(c) Flora and Faunistic Notes.

(i) Co-epiphytes and Competition: Epiphytism is a feature of common occurrence on the sea shore and reaches greatest prevalence in summer. At this time, therefore, Pylaiella faces considerable competition from various other species growing on the fronds of host plants. The chief competitors and commonest co-epiphytes with Pylaiella are Elachista fucicola Enteromorpha spp., Polysiphonia lanosa and Ceramium rubrum.

Because of their much smaller size, Elachista plants are less commonly removed from the host plants by wave action than are those of Pylaiella. This enables the species to survive as an epiphyte throughout the year and gives it the advantage of being well grown before the young Pylaiella plants start to develop. The species of Enteromorpha, usually E. compressa and often accompanied by E. linga, commence growth on the host plants

in spring along with the Pylaiella but their greater powers of reproduction and faster rate of growth often results in the shading and eventual smothering of the Pylaiella individuals. Polysiphonia lanosa and Ceramium rubrum are common but less active competitors. They are also common on the host plants throughout the year but this advantage is offset by their slow rates of growth. Indeed, their relatively robust habit occasionally permits the Pylaiella to grow on their own branches. Other common epiphytes and competitors of Pylaiella are Ulva lactuca, Ectocarpus confervoides, E. fasciculatus, Acrochaetium spp. and many species of diatoms.

(ii) Constancy of the Epiphytism. The Pylaiella plants of size and form that after some observation one begins to recognise as typically epiphytic are rarely found growing otherwise. Occasionally in the neighbourhood of a luxuriant epiphytic growth, specimens can be obtained growing on rock and other surfaces, such as the horny exoskeletons of colonial Hydrozoa. These are unusual conditions but it should be repeated that close scrutiny of many plants and numerous culture experiments with zoospores give no reason for doubt that the relationship is other than truly epiphytic.

(iii) Ascophyllum nodosum. This species, according to most workers, is one of the most important hosts for epiphytic Pylaiella and the investigations of Knight (1923) and Kylin (1933, 1937) have shown that at the Isle of Man and Kristineberg,

respectively, it plays a vital part in the life cycle of its epiphyte. Neither of these observations is true for St. Andrews where Ascophyllum is one of the more uncommon hosts for Pylaiella Dunn (1939) has already recorded this and Damman (1932) found that on Heligoland the Pylaiella was generally absent from the Ascophyllum. The reasons for the frequence and importance of the relationship to Pylaiella in some areas and the rarity and unimportance in others quite close at hand remains unexplained. At. St. Andrews young plants of Pylaiella are fairly often found growing on the ripe receptacles of Ascophyllum in spring and as these are shed after fruiting in May and June, many Pylaiella plants must certainly be lost. In addition, the vegetative parts of Ascophyllum lack the cryptoblasts which with the protruding paraphyses break the surfaces of the thalli in Fucus spp. and thus offer a convenient trap for zoospores.

These facts, however, offer only a partial explanation of this feature in the distribution of epiphytic Pylaiella.

(iv) Fauna. The two animal species most frequently associated with epiphytic Pylaiella are the sedentary Annelids, Spirorbis spirillum and Pomatoceros triqueter. These form their spirally shaped calcareous shells on the fronds of Fucus spp. but their presence does not seem to affect the growth of Pylaiella. They are both filter feeders and present in large numbers might exert a very slight control on the number of algal spores reaching and settling on the host thallus.

The ubiquitous Marinogammarus marinus is fairly common and species of Rhabdostyla and allied genera are frequently found attached to the cells of Pylaiella. In high summer when Pylaiella is found as an epiphyte on Laminaria digitata it is commonly accompanied by the mollusc Patina pellucida. This mollusc is an efficient feeder and browses intensively on the stipes and fronds of Laminaria plants. It is therefore highly probable that many young Pylaiella plants do not reach maturity solely because of the attentions of this species.

Nematode worms and unidentified crustacean larvae and innumerable flagellates complete the list of commonest associated animals.

B. WINTER-SPRING DISTRIBUTION.

(a) Description.

The autumn storms at St. Andrews and Isle of Man remove most of the population of epiphytic Pylaiella and Knight found that the few survivors bore the responsibility for producing the new season's growth. This, however, is not the case for St. Andrews. During September and October another crop of plants appears in pools at high water of neap tides or a little below this level. (Fig. 34). Since these individuals start to grow shortly after the maturation and death of the summer crop it seems likely that they originate here and develop from zoospores released in August.

The pool inhabiting Pylaiella seems to have a slightly wider range of hosts than the plants of the summer crop. Again, however, Fucus vesiculosus is the most frequent host plant with Cladophora rupestris and Fucus spiralis equally often but both slightly less commonly colonised. Fucus serratus, Halidrys siliquosa and Ceramium rubrum occur as fairly common hosts and together with the previous species bear nearly all of the Pylaiella population. A few other species such as Asperococcus fistulosus, Ascophyllum nodosum and Lithothamnion lenormandii have been recorded as hosts for Pylaiella but such instances are only very occasional.

Apart from the host species, Pylaiella in pools is associated with a flora of fairly constant and characteristic composition. The restriction of the population to the high level pools tends to ensure this. On the other hand, variation in depth and degree of exposure to light tend to favour at one extreme shade loving algae like Membranoptera alata or at the other only a rich growth of Enteromorpha and Ulva. The following species probably represent the chief associates of Pylaiella in a typical pool during the winter-spring phase of its distribution.

Chlorophyta

Enteromorpha compressa (L.) Grev.

Enteromorpha linza (L.) J.Ag.

Ulva lactuca L.

Chaetomorpha melagonium (Web. et Mohr.) Kütz.

Cladophora rupestris (L.) Kütz

Phaeophyta.

Ectocarpus confervoides (Roth.) Le Jol.

Laminaria saccharina (L.) Lamour

Sphacelaria radicans (Dillw.) Ag.

Sphacelaria britannica Sauv.

Cladostephus spongiosus (Huds.) Ag.

Asperococcus fistulosus (Huds.) Hook

Fucus spiralis L.

Fucus serratus L.

Fucus vesiculosus L.

Halidrys siliquosa (L.)Lyngb.

Ascophyllum nodosum (L.) Le Jol.

Rhodophyta

Rhodochorton rothii Naeg.

Catenella repens (Lightf.) Batt.

Phyllophora membranifolia (Good et Woodw.) J.Ag.

Chondrus crispus (L.) Stackh.

Rhodophyta (cont.)

Polyides caprinus (Gunn) Papenf.

Hildenbrandia prototypus Nardo.

Corallina officinalis L.

Lithothamnion lenormandii (Aresch.) Fosl.

Lomentaria articulata (Huds.) Lyngb.

Rhodymenia palmata (L.) Grev.

Ceramium rubrum (Huds.) Ag.

Plumaria elegans (Bonnem.) Schm.

Membranoptera alata (Huds.) Stackh.

Polysiphonia nigrescens (Sm.) Grev.

Rhodomela confervoides (Huds.) Silva

(b) Environmental Factors.

The conditions of environment are very different, and in many respects more difficult, for an alga living in a pool from one living on the open shore. Because the distribution of Pylaiella in this environment is strictly seasonal, it would seem that only those conditions obtained in winter and spring favour its growth. In addition, certain rock pools that seem wholly adequate for a good growth of Pylaiella never, or only rarely, contain specimens. The presence of Pylaiella in a pool and its ability to thrive therein depends therefore on a delicate balance of factors. The following appear to be the most important of these.

(i) Period of Exposure. The greatest density of the Pylaiella population is found in pools at and a little below H.W.N.T. Mean tide level almost certainly constitutes the lower limit for the species at this time of the year. The period of exposure experienced by the average pool is therefore in the neighbourhood of sixteen hours in every twentyfour. Some pools at the upper limit of the distribution may not be inundated during a period of low neap tides but most are covered by every tide.

(ii) Depth. The minimum depth of pool observed to support a growth of Pylaiella is about fifteen centimetres. It seems likely that this depth requirement is connected with the general stability of the environment. For example, a shallow pool, especially at high water, is liable to excessive pH and temperature fluctuations and may, under exceptional circumstances become completely dried out, whereas a deeper pool more usually contains a sufficient volume of water to buffer such changes and prevent complete evaporation. It is also probable that a depth of about fifteen centimetres has a similar control over the distribution of Fucus and Halidrys which are the most common hosts.

(iii) Temperature. Water temperature in an exposed tidal pool follows air temperature to an extent never reached by the sea. During spells of cold weather the surface layers in Pylaiella pools have frequently been observed to freeze over

while in warm days in early summer the temperature of the same layer may reach 20°C. The former condition has no visible effect on the growth of Pylaiella, but the latter, associated as it is with the disappearance of the species is assumed to be at least indirectly harmful.

(iv) Light. This is probably the fundamentally important factor in this phase of the Pylaiella distribution. It is the light requirement which brings the greatest density of epiphytic plants from the summer habitat to the high level winter pools, for, though adaptable to most habitats, Pylaiella as a species is found growing best in well illuminated areas. The same light factor, however, is responsible for the disappearance of the alga. The sudden increase in lenght and strength of daylight in spring triggers off a growth of Chlorophyta all over the shore and this growth is especially evident in high level pools where the Pylaiella is quickly smothered in a growth of Ulva lactuca, Enteromorpha intestinalis and other similar algae. The increasing temperatures associated with the light factor seem to contribute to this growth of green algae.

(v) Hydrogen Ion Content. This factor, too, depends on the light intensity. The pH of sea water at St. Andrews is around 8.4 but the process of photosynthesis by algae in a restricted body of sea water may raise this level considerably. Members of the Chlorophyta such as Enteromorpha and Ulva have been

found to be the most active, photosynthetically and on one occasion the water in a shallow pool containing a luxuriant growth of Ulva lactuca was found to have a pH of 9.2. Such increases are detrimental to the Pylaiella.

(vi) Presence of suitable hosts. As a factor of great importance this is obvious and has already been discussed.

(vii) Wave Action. This factor is of less significance than to the Pylaiella in the previous communities since most of the well colonised pools are also rather sheltered. Wave action, however, does remove a considerable proportion of the Pylaiella and if severe can cause the disappearance of large numbers of host plants.

(viii) Salinity. In a few of the high level pools there is a continuous entry of fresh water. In volume this is never more than a trickle and probably never reduces the salinity by more than 10%. This reduction in salinity has no effect on the Pylaiella itself though is very detrimental to the Fucus spp. and consequently severely restricts the available hosts (Fucus ceranoides is not common on the open shore).

(ix) Turbidity. This is generally not a factor of great importance.

(x) Dissolved Organic Substances. As before.

(xi) Dissolved Oxygen. Fischer-[illegible] (1929) described a steady rise in oxygen concentration in pools during periods of exposure in daylight, to a point of super saturation. Certainly on a bright day, bubbles of gas can be seen rising from growths of Ulva and Enteromorpha, and it may be that this excessive concentration is toxic to the Pylaiella, and contribute to its removal from pools in late spring.

(c) Flora and Faunistic Notes.

(i) Epiphytes. Algal growth is slow during winter and presumably because of this the Pylaiella is very free from epiphytes except diatoms and Phormidium fragile. The commonest epiphytic diatoms are species of Navicula, Licmophora, Grammatophora, Melosira and Cocconeis.

(ii) Co-epiphytes and Competition. As with the summer-autumn material.

(iii) Constancy of Epiphytism. The Pylaiella in pools is almost always epiphytic and only very occasionally spreads to other substrata.

(iv) Fauna. This can be regarded as identical to that associated with the summer-autumn plants, though it probably contains large numbers of Marinogammarus and fewer of the Chironomid larvae.

4. Harbour Community.

(a) Description.

The harbour at St. Andrews is small and of simple construction. It is divided into two parts, roughly equal in size, the outer being separated from the inner by a lock type gate which, however, is rarely closed. The long arm of the pier projects into St. Andrews Bay in an easterly direction curving very slightly to the south, and this, together with a short arm running north-east from the other side of the harbour, forms the entrance. At the same time these give almost complete protection from wave action.

The harbour is also the outlet for the Kinness Burn, a stream of moderate size, which effectively lowers the salinity of the water. During the years, this stream has also carved a gully in the great mass of silt which it has deposited on the floor of the harbour. At low tide it provides the only water in the upper harbour and at low spring tides the sea also leaves the outer part. The harbour is seldom used and even more seldom cleaned.

Reference to Pylaiella growing on wharves and in harbours is widespread in literature and since such places are frequently outlets for fresh water the conditions at St. Andrews must often be obtained. Farlow (1891) has reported this for New England, Kjellman (1890) observed Pylaiella in both normal and weakly saline sea water and Børgesen(1908) found the

species growing abundantly at the outlets of streams. Damman (1932) and Knight (1923) located the species in the harbours of Heligoland and Port Erin respectively, and Taylor (1957) reports it growing in quiet brackish waters of north Masachusetts. A recent and detailed study of the flora of a harbour similar to that of St. Andrews has been made by van Hoek (1958) at the Hoeck van Holland. He studied the North Pier, a structure which is washed on its south side by the Nieuw Waterweg and on the north by the North Sea, and observed Pylaiella growing abundantly all the year round, but only on the latter side. It appears then, from his observations, that Pylaiella required conditions of fairly high salinity and low light intensity for active growth. None of these observations on the distribution of Pylaiella hold good for St. Andrews where its presence in the harbour is strictly seasonal and where it can be found growing well in areas receiving full sunlight and in water with a salinity of less than two parts per thousand.

The Pylaiella population is almost exclusively restricted to the more weakly saline water of the upper harbour and about half of this is epiphytic on Fucus ceranoides, the remainder occurring on stones, piles or any other stable objects. This situation is in sharp contrast to those among the other communities on the shore where a Pylaiella population is

either exclusively lithophytic or exclusively epiphytic. Since growth, in the harbour, is equally robust on Fucus and on stones, the epiphytic relationship would again seem to be completely non-parasitic in nature.

The season of harbour Pylaiella growth extends over a period of nine months. The first plants can be observed growing in the upper harbour at the end of October or beginning of November and at this time they are approximately 2 - 5 cm. in length. They grow fairly slowly until March or April after which the growth rate increases enormously and by June they are at maximum size. The plants are immense with an average frond length of 30 cm. while the largest specimen measured was 91 cm. in length.

In form they are lacking in good cable strand development. This results in a thallus of limp texture and disorganised appearance (Fig.35). The large thallus size puts considerable strain on the rhizoidal filaments and during July the entry of every tide causes the removal of great numbers of plants most of which are washed out to sea. By August the population has entirely disappeared except for a few small tufts on Fucus ceranoides.

The fertility of the harbour plants is low and all examined plants were found to bear unilocular sporangia alone, in chains of up to thirteen in number, and frequently quite solitary.

The range of species in the upper harbour is much smaller than in the other communities so far described. Fucus ceranoides is the chief associate as well as the commonest host and the two species occur together during the nine months of Pylaiella growth. In March they are joined by species of Enteromorpha, usually E. intestinalis with a little E. compressa and for the rest of the summer Pylaiella, Fucus ceranoides and Enteromorpha are the dominant algae. Urospora speciosa, Cladophora rupestris, Elachista fucicola, Sphacelaria britannica and Porphyra liciniata and the diatoms Lauderia borealis and Navicula spp.(in schizonema tubes) and a species of the blue-green Dermocarpa complete the list of commonest species.

The Pylaiella at maximum distribution extends a little way into the outer harbour and here the above mentioned species are joined by several, more marine, algae. The chief of these are Pelvetia canaliculata, Fucus spiralis, Ascophyllum nodosum (on which this Pylaiella has been recorded as an epiphyte), Polysiphonia lanosa and Catenella repens.

(b) Environmental Factors.

(i) Salinity. This is obviously a factor of extreme importance. Salinity was measured on several occasions and found to be dependent on the height of tide and condition of the river. When a rising tide enters the harbour it naturally fills up first the gully containing the stream and, because the sea

water is more dense than the fresh, carries on its surface a layer of nearly saltless water. This surface layer then spreads over the gently sloping mud banks which constitute the remainder of the harbour floor and area of most Pylaiella growth. The mixing of the waters is never complete but is naturally more efficient during periods of rough seas.

The Pylaiella is covered by water of lowest salinity when high water of a neap tide coincides with the river in a condition of spate. High spring tides coinciding with a low river provide conditions of maximum salinity. Data illustrating this are given below. Samples of water were taken from the upper harbour at high tide and at depths of 25, 50, 75, and 100 cm. respectively. The salinities were measured by hydrometry, converting by means of Knudsen's Hydrographical Tables.

Table I.

Height of Tide.	Depth of Sample	Salinity	River Condition
12.2 feet (Neap)	25 cm.		Moderate Spate
	50 cm.	3.78°/oo	
	75 cm.	17.75°/oo	
	100 cm.	26.69°/oo	
15.4 feet (Spring)	25 cm.	27.64°/oo	Low
	50 cm.	30.13°/oo	
	75 cm.	30.13°/oo	
	100 cm.	30.14°/oo	

Since the bulk of the Pylaiella population grows quite high up on the mud banks it probably receives during neap tides water with an average salinity of 5°/oo at the upper part of its distribution and 20°/oo at its lower limits. During spring tides the figures for the same limits are probably 25°/oo and 30°/oo respectively.

The direct effect of this low salinity on Pylaiella is certainly not harmful to vegetative growth but may inhibit fertility as the plants form very few sporangia. Indirectly, it is beneficial as it reduces the number of competing species effectively to two, Fucus ceranoides and Enteromorpha intestinalis, and of these, the first is a valuable host plant.

(ii) Dissolved Oxygen. The dissolved oxygen concentration in the harbour is probably lower than that in the sea, but whether it is low enough to affect the Pylaiella or not is unknown, but thought to be unlikely.

(iii) Period of Exposure. Pylaiella in the upper harbour grows on the mud banks that slope gently down to the gully containing the Kinness Burn, the stream itself and the steep sides of the gully are seldom colonised. High water of a poor neap tide leaves less than one quarter of the population uncovered and an average spring tide covers all of it to a depth of 50-100 cm. The mud very rarely becomes dry, and for the Pylaiella plants spread fan-like on its surface there is usually enough moisture present to prevent desiccation.

(iv) Light. This appears to have little destructive effect on the Pylaiella, contrary to the findings of van Hoek (1958). At the upper limit of its distribution and in conditions of strong sunlight, plants have been observed in a fairly dry condition, but never fatally desiccated. In June and July, however, some of the plants which are removed from their substrata are cast up on the various grasses which grow on the margins of the barbour. In this environment and under strong sunlight they are rapidly killed.

(v) Wave Action. This is negligible in the upper harbour, and the water movement that causes the removal of the Pylaiella plants in summer is not so much wave action as mere tidal ebb and flow.

(vi) Ice Action. Surprisingly, this is quite an important factor. Because of its low salinity the surface layer of the harbour water readily freezes in winter and during periods of low tide sheets of ice come to lie on top of the young Pylaiella plants. The rising of the tide causes these to grind against one another and the mud so that many of the young plants are dislodged and carried away.

(vii) Temperature. The river temperatures in winter are lower than those of the sea and, in exceptionally cold periods, may reduce the temperature of the harbour water from the sea minimum, which is about 4°C., to below freezing point, at least in the surface layers. In summer, the upper water layers

may become correspondingly higher. The low temperatures do not seem to affect the Pylaiella and the high summer ones are not directly harmful but may be indirectly so, because the latter favour the growth of Enteromorpha spp. and hence increase space competition.

(viii) Hydrogen Ion Content. This was measured on several occasions and found to be lower than that of the sea. The average pH of surface water in the harbour is about 8.0 with lowest readings in winter (about 7.8) and rising to 8.2 in summer under conditions of maximum growth and photosynthetic activity. As a factor it does not seem to be of great significance.

(ix) Substratum. Many of the non epiphytic Pylaiella plants appear to grow directly on the mud surface and where this is reasonably stable, a few do so. In general, however, most of these plants when examined carefully can be found to be attached to small stones lying just under the mud surface. It seems, therefore, that the plants prefer a stable substratum.

Although the mud particles are very fine and easily disturbed, the Pylaiella fronds with their large limp construction and low weight to frond-area ratio lie easily on the mud surface.

(x) Turbidity. This is undoubtedly greater than in the sea but does not seem to affect the Pylaiella much and may, by

the abrasive action of the particles, keep the filaments free of epiphytes. It does, however, produce a deposit of silt which often accumulates on the fronds of Fucus ceranoides, thereby providing conditions for active growth among various micro-organisms which, in turn, cause harm to the fronds.

(xi) Dissolved Organic Substances. A greater concentration of these substances occurs in the harbour than in the sea but their effect is not evident.

(c) Flora and Faunistic Notes.

(i) Epiphytes. The Pylaiella plants in this community are remarkably free from epiphytes, due possibly to the scouring action of the mud particles, but more probably to the restrictive effect of the environmental conditions on the number of algal species capable of living there. Nevertheless the blue green Phormidium fragile is again common along with several diatoms of which the most frequent is Lauderia borealis.

(ii) Fauna. The commonest animals in the upper harbour are Marinogammarus marinus, Mytilus edulis, Nematode worms and flagellates.

5. Salt Marsh Community.

(a) Description.

About three miles from the town of St. Andrews the River Eden flows into the sea. The estuary which is about one mile across has a small area of saltmarsh on its south bank. The dominant species on this salt marsh is Festuca rubra and the areas of this plant are broken up, here and there, forming channels and salt pans. Specimens of Pylaiella can be found in these salt pans throughout the year.

Dunn(1939) has reported this growth of Pylaiella, and as she suggests this estuarine habitat is similar to that described by Chapman (1937) for Norfolk. Rees (1935) on Lough Ine, Ireland, reports a "salt marsh subformation" which, although lacking Pylaiella, contained two species of Ectocarpus. In all other respects it was identical with the Eden estuary salt marsh and it must be concluded that Pylaiella is not uncommon in such habitats.

The salt marsh Pylaiella is free living. Some specimens seem to be attached directly to the mud or Festuca rhizomes but close examination shows that their filaments are only entangled with one another and those of other algae (Fig.36). The plants are impossible to measure since they completely lack form or filament organization. There is practically no cable strand and the tufts are hopelessly intertwined.

This free living condition raises the problem of origin. Dunn (1939) has observed Pylaiella plants growing also on the mud flats of the Eden estuary itself. This has not been observed by the author but such a growth, similar probably to that of the harbour, would provide the likeliest reservoir from which the salt marsh material could be derived. Otherwise it must come from the storm detached harbour or epiphytic plants. The fact that the species is commonest in autumn would tend to support this.

Most of the examined tufts proved to be fertile with unilocular sporangia predominating. They are found in chains of up to fifteen in number with an average figure of eight.

Typically the Pylaiella occurs entangled with great masses of Enteromorpha compressa or E. intestinalis, and, like the Pylaiella, both these species are free living. Other common free living algae are Fucus spiralis, F. ceranoides, F. vesiculos Enteromorpha linza and Porphyra liciniata.

The mud walls of the salt pans are stabilised by the root and rhizome development of Festuca rubra and bear a characteristi growth of creeping filamentous algae. The most important and common of these are Vaucheria sp., Calothrix consociata, Microcoleus chthonoplastes, Percursaria percursa and Sphacelaria radicans.

Apart from the Festuca some other Phanerogams commonly occur with their roots or rhizomes twined and festooned with

Pylaiella. Commonest of these are Aster tripolium, Glaux maritima, Plantago maritima, Salicornia stricta and Cakile maritima.

(b) Environmental Factors.

Since the Pylaiella arrives at the salt marsh in a more or less mature condition and as its distribution is haphazard and its presence temporary, it is difficult to relate its development with the obtaining environmental factors.

Briefly, however, wave action, or more accurately wave direction, is obviously the most important since it carries the population to and from the habitat. Salinity is low due to the mixing of sea and river waters (average salinity 16.6$^{o}/_{oo}$) and though it rises steadily during the period of exposure of a salt pan, it never reaches the concentration normal for sea water. The pH follows a similar range to that obtained in the harbour (it is also low) as do the temperatures. The amounts of dissolved oxygen and organic substances are almost certainly lower and higher, respectively, than those in the sea. Although these conditions are associated with stagnation and decay of algae (which are common features in salt pans, especially in summer), they constitute factors of no apparent significance.

(c) Faunistic Notes.

(i) Fauna. Certain animals, usually molluscs such as Mytilus

edulis, Cardium edule and Nucella lapillus, occasionally accompanied by small Arthropods, are carried into the salt pans with the larger algae. They are never able to endure the conditions for long and, in summer, generally die within a few days. The indigenous fauna is composed almost exclusively of flagellates and other micro-organisms.

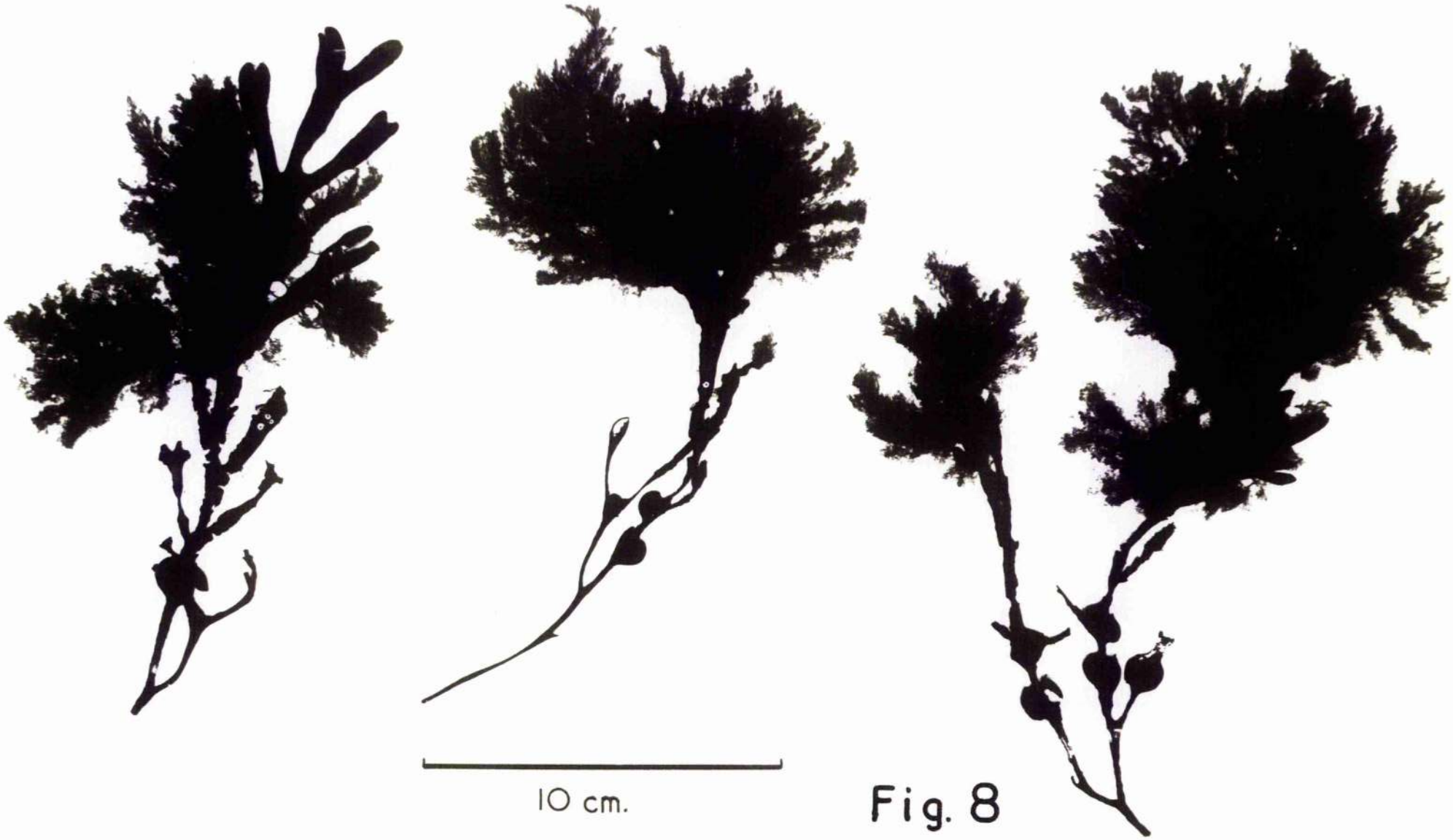
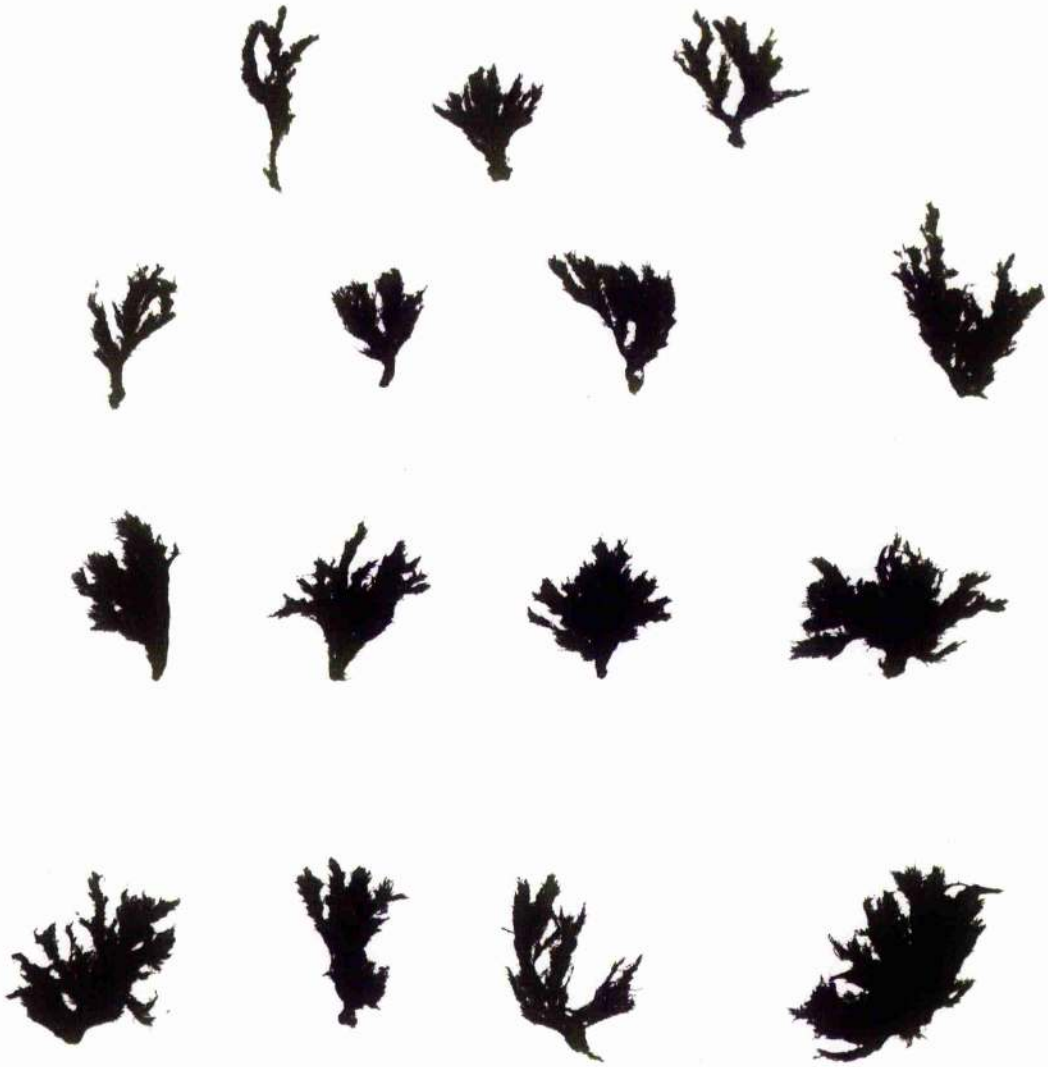


Fig. 8



10 cm.

Fig. 7

VII. COMPARISON OF P. LITTORALIS IN ITS VARIOUS COMMUNITIES.

1. Morphological Differences.

Figs. 7 , 8 , and 9 , show herbarium specimens of typical Pylaiella from lithophytic, epiphytic and harbour growths respectively. It is obvious that the plants differ enormously in appearance. It is not at all easy, however, to describe these differences in quantitative terms. This is the problem which makes taxonomic and experimental work on the filamentous Ectocarpaceae so difficult. In the previous section brief reference was made to the differences in form at St. Andrews; these should now be considered in greater detail. It is not proposed to discuss the Pylaiella from the boulder or salt marsh communities. These are small both in size and importance in the total distribution.

The herbarium sheets show that the lithophytic plants are small (average frond length 1.8 cm.) and sturdy with a very prominent cable strand development bearing relatively short branches. The frondsare dark brown in colour. Epiphytic plants, while showing no difference in colour from the lithophytic, are much larger in size (average frond length 15cm.). They show a similar development of cable rolling but a greater profusion of much longer branches. Finally, in the harbour specimens we have the largest plants of all (average frond length 30 cm.) showing a poor development of cable rolling giving off long branches of a rather pale brown colour.

10 cm.

Fig. 9

Microscopic examination, however, does not substantiate these differences in appearance. The differences in frond length are not accompanied by similar variation in cell size. For example, the measurements of certain microscopic features in the structure of Pylaiella are given below, the averages being calculated from about fifty measurements on several plants in each case.

Table 2.

	Lithophytic Plants.	Epiphytic Plants.	Harbour Plants
Average cell wall thickness	2.9 μ	1.9 μ	2.0 μ
Average cell diameter in main filaments.	27 μ	29 μ	28 μ
Average cell length	1.5 x diam.	1.5 x diam.	1.0 x diam.
Average cell diameter in ultimate branches	16 μ	11 μ	18 μ
Average cell length	2 x diam.	2 x diam.	2 x diam.

These figures in themselves show no real differences between the plants but when one examines the possible range in size for any of these criteria, this is even more so. For example, in the lithophytic plants, the range of cell wall thickness is from 1.5 μ to just over 3 μ, in the diameter of main filament cells from 22 μ to 33 μ, and in the ultimate branches from 12 μ to 20 μ. The same can be observed in all

plants from various communities for any of the above criteria.

Observation of Pylaiella throughout the period of investigation showed differences in the types of sporangia borne by the species in the different habitats. The lithophytic plants bore unilocular sporangia exclusively during the winter months and both types simultaneously in summer. Epiphytic plants also bore both types of sporangia but with a predominance of pluriloculár in summer and unilocular in winter, while harbour plants produced unilocular sporangia alone throughout their growth season.

Unilocular sporangia were produced in greatest numbers by the lithophytic plants on which they occurred in chains of up to twenty five in number. On epiphytic plants this number fell to about fifteen while on the relatively sterile harbour plants the longest recorded chains was of thirteen sporangia, but this figure was uncommonly high, the average being about eight. In dimensions, however, the sporangia did not differ greatly. The average unilocular sporangium on a lithophytic plant had a breadth of 32μ and a length of 30μ but the following examples, 26.5μ x 32μ , 40μ x 51μ and 43μ x 42μ give some idea of the variability. Epiphytic plants, on the average, bore sporangia 29μ in breadth and 26μ in length but again 32μ x 43μ , 33μ x 28μ and 16μ x 26μ were observed dimensions. Among the harbour plants the average unilocular

sporangium was 30μ broad x 27μ long but size ranged from 22μ x 24μ to 38μ x 37μ .

In all cases only mature sporangia were measured. The ejectory papillae which form on the sides of ripe sporangia had an average height of 3.0μ , a figure common to plants from all communities.

Plurilocular sporangia on lithophytic plants ranged from 29μ to 53μ in diameter and from 59μ to 142μ in length. On epiphytic plants they were somewhat larger with an average diameter of 40μ (range 31μ to 64μ) and length of 250μ (range 135μ to 352μ).

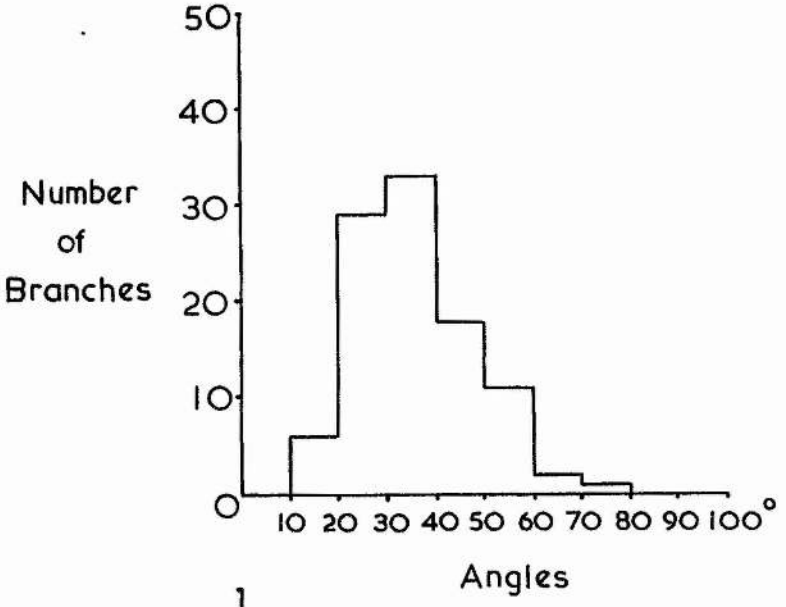
The apparent differences in branching between the plants were not borne out by examination and no semblance of regularity or pattern could be found in any plant from any community. Camera lucida drawings of the angles of branch emergence were made from many plants sampled from each community (100 angles measured in each sample). The results are presented in Fig.10 and it can be seen that the histograms show only slight differences in form and distribution. The mean angle of branch emergence in lithophytic plants is 36.4°, in epiphytic 35.9°, and in harbour 35.1°, again very similar figures.

The differences in the appearances of the plants can be expressed if the dry weights of the fronds per square centimetre of area are compared with one another. This measurement was

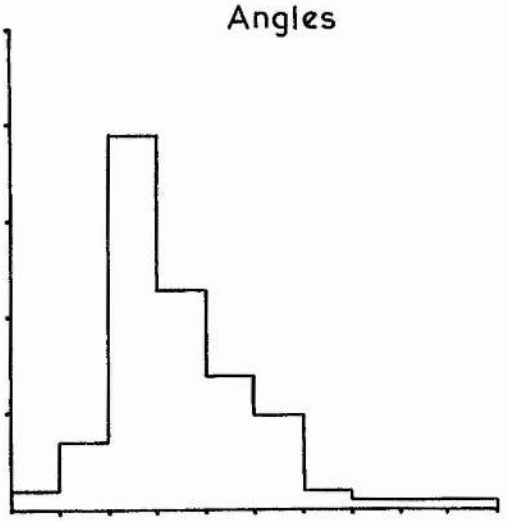
Angles of Branch Emergence in Pylaiella littoralis (L.) Kjellm.

at St. Andrews

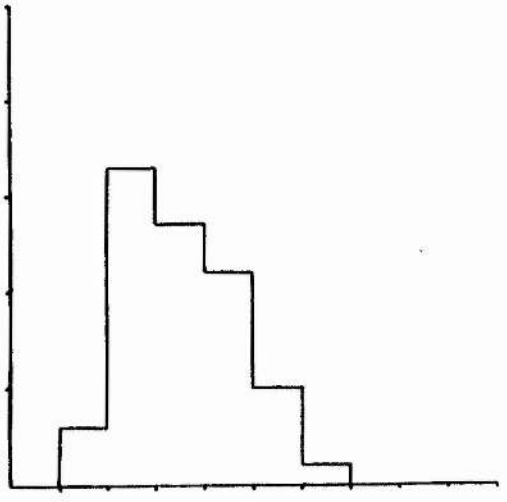
100 Measurements per Sample



Rock Plants



Harbour Plants



Epiphytic Plants

Fig. 10

found by selecting a number of plants of various sizes and stages of growth from each environment. Each plant was rinsed free of grit in distilled water, laid flat out on centimetre graph paper and the outline of the frond drawn. The plants were then transferred to weighed aluminium foil boats and dried at a temperature of 95°C. for three days.

The short dense habit of the lithophytic plants was expressed by a dry weight of 0.0031 gm. per square centimetre of frond, the larger, more widespread fronds of the epiphytic material had a ratio of 0.0022 and the limp, disorganized growth of the harbour specimens weighed 0.0012 gm. dry weight per square centimetre. In range the epiphytic and lithophytic plants overlapped slightly but both were above the upper limit of the harbour plant range.

2. Experimental Differences.

Several simple experiments have shown some degree of dissimilarity in the plants from the three communities.

(i) Field Transplants.

Pylaiella material was transplanted throughout the year from each community to the others. Pieces of stone bearing growths of lithophytic material were chiselled from the sandstone ridges and the pieces placed in pools containing epiphytic Pylaiella, on areas of open shore and on the mud of the upper harbour. Epiphytic and harbour materials were likewise transplanted.

Lithophytic plants were found to retain their size and form in all "foreign" areas, while in the harbour they became rapidly coated with silt and infested with micro-organisms, and died not later than four weeks after transplanting. Epiphytic material was too quickly removed by the surf from the areas of lithophytic growth to give any concrete result but at no time showed any alteration in form. When grown in the harbour it suffered the same fate as the lithophytic plants. Harbour inhabiting plants were transferred on many occasions but their limp frond construction could not withstand even the most moderate wave action and were inevitably removed by the first high tide.

(ii) Culture Experiments.

An attempt was made to overcome the difficulties of transplanting material in the field by repeating the experiments in culture. This involved growing pieces of adult plants from each of the three communities in Erd-Schreiber culture medium. Two types of the medium were prepared, one based on inshore sea water, as prescribed, and another based on the less saline water of the harbour. After a period of one month none of the lithophytic specimens had shown any increase in length whatsoever while the harbour and epiphytic specimens had grown but by varying and rather inconclusive amounts. It was thought that the lack of growth by the lithophytic plants might have been due to the absence of aeration in the culture conditions

but an experiment involving the same material submitted to continuous aeration gave no different results.

Following these experiments another more critical one was devised in which adult plants from the three communities were cut up into very small lengths of filament. These consisted of no more than fifty cells with a probable average of twelve cells. The minced up material from each community was then shaken up in a test tube with filtered sea water and about 1 cc. of the suspension pipetted into deep petri dishes containing three types of Erd-Schreiber culture solution. These were made up from harbour water, from sea water as prescribed, and from sea water but enriched with twice the recommended amounts of phosphate and nitrate. The experiment was carried out under continuous fluorescent lighting and at a temperature of 10°C ± 1°C.

After a period of one month it was found that the epiphytic plants possessed, under these conditions, the greatest ability to regenerate. The culture solution in which this occurred to the maximum degree was the one based on sea water and containing extra phosphate and nitrate. In this solution the tiny fragments of filament had grown into small plants up to 3 mm. long showing cable rolling, development of rhizoidal filaments and profuse branching. They also bore unilocular sporangia many of which had already dehisced. The culture solution

based on harbour water promoted least vegetative regeneration and poorest sporangium formation, none of the sporangia having dehisced. The normal Erd-Schreiber solution gave intermediate results, the plants being not quite so large or fertile as in the first.

The lithophytic material showed the least capacity for regeneration, the fragments doubling or trebling in cell number and branching to a fair extent but showing little organization into complete plant form. As with the epiphytic material, the culture solution which provided optimum conditions was the enriched Erd-Schreiber and in this the Pylaiella produced considerable numbers of unilocular sporangia. On the other hand the culture medium based on harbour water promoted least vegetative development and no reproduction. The normal solution again gave intermediate results.

The harbour inhabiting plants varied from the other two types in their response to the culture conditions. They showed almost as much capacity for vegetative regeneration as the epiphytic material but with no marked difference in amount of growth between the plants in the three media. The fertility of the little plants was lower than of the other types and was equally low in all three media.

These results considered as a whole would tend to suggest that the form differences between the plants from the main

communities are associated also with certain physiological differences. It seems likely however that variation in fertility, at least, is due to certain environmental conditions of which low salinity seems the most effective inhibitor.

VIII. SUB SPECIFIC TAXONOMY OF P. LITTORALIS

The variations in appearance of the Pylaiella from its several habitats at St. Andrews have been discussed. Such differences have been observed all over the northern hemisphere and numerous attempts have been made to accommodate them somehow into the system of orthodox taxonomy. The resulting confusion of subspecies, varieties and forms has strained the system beyond the limits of usefulness, and the ambiguity of the descriptions has made identification of any given specimen almost impossible.

Kjellman (1890) in his Handbook gave a detailed taxonomy of P. littoralis and in most cases this was accepted as the basic classification into which, if necessary, other units were placed.

Kjellman describes three varieties of P. littoralis, var. opposita, var. firma and var. divaricata, each with five, four and four forms respectively. Var. opposita has the

erect shoot branched "in a regular way; the branches mostly opposite". The plant is "tuft like" and "bushy" the branches of which "below are loosely twisted together and at the top are fluffy or unentangled". In colour it may be equally yellow brown or rust brown, 5 to 20 cm. in frond length and equipped with plurilocular sporangia 100μ - 300μ long and ranging from 25μ - 75μ in diameter. This is the forma typica from which he differentiates f. rupincola with smaller, more dense tufts, a rather darker colour and with unilocular sporangia in chains of varying length and plurilocular sporangia which may be terminal in position. Next he describes f. elongata, "tufts are loose.....yellow brown.....plurilocular sporangia are longer and thinner than in main form. Usually they are more than 300μ long and 20μ - 25μ in diameter". Then comes f. crassuscula, "small and tuft-like, pale brown and with short and thick plurilocular sporangia. These are cylindrical to cylindrically fusiform and sometimes situated terminally". And lastly for var. opposita he described f. nebulosa which has shoots "more or less felted together....loosely branched. The branches are mostly opposite".

In this vein he ascribed to var. firma an f. typica, a f. divacea, f. macrocarpa and f. parvula, while to var. divaricata a f. typica, f. praetorta, f. aegagropila and f. subsalsa. He also describes with these varieties and

forms of P. littoralis a P. nana, a P. varia and a P. curta.

Some twelve years later, Børgesen (1902) in his study of the flora of the Faeroes recognised specimens from the three varieties of Kjellman but he identifies them with several forms not mentioned in the Handbook. In addition to the forms of var. opposita we now also have a f. subverticillata Kuck. and f. rectangulans. Var. firma has an additional f. subglomerata Kuck. and var. divaricata a f. ramellosa Kuck. while Kjellman's P. varia is reduced to a variety, the number of varieties at this time therefore being at least four.

This situation must have been most unsatisfactory and it is not surprising that Knight received much support when in 1923 she claimed that the different forms of Pylaiella arise simple by the processes of growth, reproduction and ageing of plants together with the effects of differing environments. As she points out, the release of its zooids by an intercalary sporangium leaves only the torn cell wall connecting the distal and proximal parts of the filaments. Sooner or later, this breaks and the plant in consequence suffers from what, in effect, is a continuous pruning. Thus if vegetative growth exceeds production of sporangia the shape of the plant will be somewhat different from that if the opposite holds. She observed certain individual plants throughout a growing season and claims that alterations in

form were apparent at different stages of growth. She concludes by stating that the criteria employed in the orthodox taxonomy of this species are too variable to serve as a basis for classification.

Nevertheless, the species remains classified. Setchell and Gardner (1925), while accepting the possible validity of Knight's claims, identified on the Pacific coast of North America individuals from the varieties opposita, firma, divaricata and varia. Newton (1931) also doubts whether the varieties etc. can be regarded as more than growth forms but at the same time gives short descriptions of five varieties for the species on British coasts. These are var. opposita Kjellm., var. brachiata Batt., var. longifructus Batt., var. firma Kjellm., and var. ramellosa Kuck. This now raises the number of described varieties to seven. Lastly, Taylor (1957) on the North Eastern coast of North America records var. opposita Kjellm. var. firma Kjellm., and var. varia Kjellm. and two others, var. fluviatilis Kutzing (Hauck) and var. robusta Farlow. He does add the qualification that these may well be unable to withstand critical study.

This means that there have been described at least nine varieties of Pylaiella littoralis with an unknown number of forms.

At St. Andrews the lithophytic plants are almost certainly

P. littoralis var. opposita f. rupincola Kjellm. Identification of the epiphytic material is less easy but comparison with the type specimen in the Herbarium of the British Museum suggests that var. firma Kjellm. f. subglomerata Kuck. is the nearest in appearance. The harbour material appears to be unique but Taylor (1957) describes his var. fluviatilis Kützing (Hauck) as "forming tufts 1 - 3 dm., tall, softly flexuose" with "flaccid filaments elongate, sparingly branched, the branches tapering to the apices" and reports it from northern Massachusetts "in quiet rather brackish water". The description seems very similar to, and the environment identical with that of the Pylaiella growing in the harbour. Accordingly, this is named provisionally as P.littoralis var. fluviatilis Kützing (Hauck).

Knight's claims on the growth forms in Pylaiella are certainly partly true but at St. Andrews these have not been found to be entirely so. At St. Andrews the lithophytic plants, though twice as tall in summer as in winter have precisely the same stunted sturdy appearance with much cable rolling. The epiphytic material too, is shorter and possibly slightly paler in winter than in summer but otherwise no different, while the harbour plants show the same limp, rather disorganized form throughout their lives.

Environmental factors, as Knight observes, are also very important. The lack of wave action in the harbour water undoubtedly contributes the large size of the Pylaiella found there and so does the low fertility of the of the plants (this is really an expression of the low salinity of the water). Transplant experiments and experiments in culture, however, have shown that such factors may not be exclusively or even mainly responsible.

The chief criteria used in the classification of Pylaiella are: system of branching, size of branches and angles of emergence, size of cells in main and other filaments, size, type and position of sporangia, and colour of plant. All but one of these are macroscopic features and unfortunately when the types of Pylaiella at St. Andrews are examined microscopicall there is sufficient overlap among them in any one of these features to make it taxonomically useless. This can be seen by comparing the angles of branch emergence among the plants from the three main communities (Fig. 10). The histograms show that the ranges of these angles overlap almost completely while the means of the angles are likewise not significantly different. Finally, var. opposita f. rupincola is a fairly safe identification for the lithophytic material, yet observation shows that no more than fifteen percent and almost certainly much fewer of the branches are actually opposite one another.

It seems then that Knight, though only partly correct in her claims on the origins of the forms in Pylaiella, must be regarded as justified in criticising the criteria used in their classification.

IX. PYLAIELLA RUPINCOLA (ARESCH.) KYLIN.

1. Review of Life Cycle.

In 1933 Kylin described the life history for P. littoralis on the west coast of Sweden and found a summer gametophyte on Sertularia (Dynamina) pumila alternating with a sporophyte on Ascophyllum nodosum. He also mentioned a form rupincola which he described briefly to grow on rock surfaces and to bear predominantly unilocular sporangia together with a few plurilocular sporangia. He quoted Kuckuck (1891) as claiming that both the unilocular and plurilocular sporangia occur on the same individual.

In his paper of 1937 on the same subject Kylin repeated without alteration his observations upon epiphytic Pylaiella but he now separated the lithophytic plants as a distinct species on the grounds that they lack alternation of generations. The name he chose for these plants was P. rupincola. P. rupincol he described as growing almost exclusively as a lithophyte but occasionally spreading as an epiphyte to Fucus serratus or

Fucus vesiculosus. In the latter event he always found the plants on the lower and older parts of the Fucus stipes and never, as in P. littoralis, congregated on the young upper regions of the frond. In growth he found the species to be at maximum development in spring, to be dying out in June and absent, except in shady areas for the months of July and August. The new generation appeared again in the autumn. The only visible means of discerning his P. rupincola from P. littoralis, apart from the lithophytic habit is stated to lie in the relative development of cable rolling. He claimed that P. rupincola showed a more prominent cable strand than P. littoralis.

Kylin observed Pylaiella for several years and during this time looked, without success, for a gametophyte of P. rupincola i.e. a plant bearing plurilocular sporangia alone. Almost all the specimens that he examined were found to bear chains of unilocular sporangia alone, accompanied occasionally by a few plurilocular sporangia. He confirmed Kuckuck's observation that these plants only bear plurilocular sporangia in the company of unilocular sporangia. Kylin then deduced that the species must consist of sporophytes reproducing sporophytes thereby eliminating the gametophyte phase and hence lacking alternation of generations.

This he proceeded to prove by growing the species in

culture. In July 1935 he set up cultures using the zoospores released from unilocular sporangia. By mid-December the individuals were up to one centimetre long, and fertile, but bearing unilocular sporangia alone. He compared this with similar experiments on P. littoralis in which zoospores from unilocular sporangia had germinated to form plants with plurilocular sporangia alone. P. rupincola was therefore justified in its separation as a species distinct from P. littoralis.

Damman (1930) had made a cytological and developmental study of P. littoralis from Heligoland where the species grows both as a lithophyte and an epiphyte. She had observed a reduction division in the development of unilocular sporangia but had noted that zoospores from such sporangia germinated, in culture, to form plants bearing unilocular sporangia only, or both types simultaneously. From these observations, she had concluded that haploid Pylaiella could and did bear both types of sporangia. Kylin (1937) stated that the culture experiments revealed her confusion of P. littoralis with P. rupincola, and ignoring her cytological evidence suggested that the monophasic life history of P. rupincola arose by inhibition of meiosis in the development of unilocular sporangia.

Du Rietz (1941) in a footnote to his Scytosiphon paper reviewed the speciation of Pylaiella. He did not disagree

with Kylin in his claim that what had hitherto been P. littoralis should now be either of two species but was critical of Kylin's selection of the specific name rupincola which had been borrowed from Ectocarpus firmus var. rupincola. Dur Rietz maintained that the bulk of the Pylaiella found in the Baltic area bore unilocular sporangia alone or accompanied by plurilocular sporangia. He therefore deduced that as Linneus had collected much of his material from this region that his Conferva littoralis (the progenitor of P. littoralis) must have been applied to such material. To support this hypothesis he produced a statement by Dillenius that the Conferva grew on rock. Du Rietz therefore recommended the P. rupincola of Kylin be now called P. littoralis and that the P. littoralis with its true alternation of generations be given another name. For the latter he suggested P. Kylinii.

In 1942 Kylin presented a long paper on the early history and nomenclature of Pylaiella. In this, he maintained that his P. littoralis was identical with the traditional P. littoralis and that his P. rupincola had been erroneously described in the past as Ectocarpus firmus var. rupincola. Du Rietz, he claimed, was therefore quite wrong.

Apart from the rather academic arguments on nomenclature the concept of P. rupincola as a separate species has remained undisturbed. Fritsch (1942) in his review of the algal life

cycle mentions several species in the Ectocarpaceae (including P. rupincola) in which swarmers from unilocular sporangia have developed into plants again bearing this type of reproductive organ. He regards Kylin's hypothesis, that this is due to failure in meiosis, as the most valid interpretation but adds the qualification that cytological investigation is clearly necessary.

Waern (1952) studied the rock shore algae at the Öregrund Archipelago which is on the Baltic coast of Sweden near the mouth of the Gulf of Bothnia and in his paper reviewed the status of P. rupincola. This he appeared to accept, although he also provided some information which tended to jeopardise the species. He mentioned that Kylin had (to his knowledge) now found exceptions to the described life cycle for P. littoralis, sensu stricta. Not only had Kylin found plants of this species bearing both unilocular and plurilocular sporangia simultaneously, a fact not previously recorded by him, but had also found numerous plants of the same species growing directly on rock surfaces. The latter were located in winter and observed in large numbers growing under fronds of Fucus and Ascophyllum. It is unfortunate that Kylin himself was not able to describe this situation in detail. Waern

also criticised Kylin's failure to provide any regular means of identifying the species beyond the facts that it is usually lithophytic with a well developed cable strand and a frond length of three to five centimetres. He concluded by suggesting the possibility that P. rupincola may be a postponed succession of asexual P. littoralis similar to those observed in certain red algae on Baltic shores.

Apart from these doubts of Waern, the validity of P. rupincola has remained unquestioned.

2. Ecology.

Kylin in his papers on P. rupincola concerned himself largely with life cycle and described it ecologically only to the extent of mentioning its growing typically in sheets over rock surfaces along with Fucus and Ascophyllum. It could also occur epiphytically on the latter but this was exceptional. Levring (1937) also seems to accept P. rupincola as a separate species but offers no more ecological information than Kylin. He does, however, find it growing among, and sometimes on, Patella vulgata and Balanus balanoides.

Waern (1952) describes the P. rupincola as forming a mat of vegetation around the upper limit of the Fucus vesiculosus belt and penetrating it in places where the Fucus growth is not too thick. In such places the Pylaiella is found in small isolated clumps or forming a fringe around the groups of Fucus plants. He also increases the number

of species on which it can be an epiphyte from the Fucus serratus and F. vesiculosus of Kylin by adding Dictyosiphon foeniculaceus, D. chordaria, Cladophora rupestris and Furcellaria sp. to the list.

Probably the best account of the ecology of Pylaiella rupincola is described by Sundene (1953) in his work on the algal vegetation of Oslofjord. He finds that on both exposed and sheltered parts of the coast the Pylaiella forms a well marked zone in which it is clearly dominant. This zone is in the littoral but may extend into the upper part of the sublittoral. The species is usually attached to rocks and stones but may also grow on some animals such as Balanus and Mytilus, and on the older parts of F. serratus, F. vesiculosus and A. nodosum. In all parts of the fjord he found the Pylaiella dominating a distinct association when the Fucoids are absent; otherwise it forms a leading species in the sub-vegetation of these Fucoids.

In late autumn, the rocks could be seen coated with a brown carpet composed of young Pylaiella plants which by December were at a height of about one centimetre. These persisted throughout the winter when ice action removes most of the larger algae, although growth at that time he observed to be minimal. Optimum development, he found, took place in April, May and June after which the plants tended to be colonised by various species of diatoms and crowded out by

the growth of Fucoids and certain summer annuals. The species could be observed throughout the summer, however, when its characteristic tufts remained attached to rock surfaces.

The Pylaiella associations on sheltered and exposed coasts varied little in character and in both cases the Pylaiella seemed to grow best on gentle rock slopes. Of the two associations the sheltered coast one seems to approximate more with the lithophytic community at St. Andrews. From the following species which Sundene identified as some of the components of this association it can be seen that this is so; Ulothrix flacca, Enteromorpha sp., Ulva lactuca, Chaetomorpha aerea, Cladophora rupestris, Fucus vesiculosus, F. serratus, Ascophyllum nodosum, Bangia fuscopurpurea, Hildenbrandia prototypus, Lithothamnion lenormandii, Chondrus crispus, Ceramium rubrum and Polysiphonia nigrescens.

As far as sporangial development is concerned Sundene observed that the species usually bore unilocular sporangia only although plurilocular sporangia were not infrequent. The latter type, however, were again always accompanied on the same plant by unilocular sporangia.

Also while admitting that it was often extremely difficult to distinguish P. rupincola from P. littoralis he preferred to consider them as two separate species along with Kylin. Nevertheless, in the text, he frequently refers to plants

as Pylaiella sp. in situations where accurate identification was not possible.

3. Personal Investigation.

From the above descriptions it became evident that the lithophytic plants of P. littoralis at St. Andrews were, if not P. rupincola, certainly very similar to it in habit, growth, associated species and sporangial development. It was therefore decided to investigate this species as thoroughly as time permitted. Contact was made with the zoological station at Kristinberg (Kylin's old collecting area) and from there Dr. Mats Waern kindly sent off a few specimens of P. rupincola. This was packed fresh and slightly damp in a polythene bag and sent by airmail. It arrived in good condition on the 29th October, 1958. Some of the material was placed immediately into Erd-Schreiber culture solution enriched as previously described and kept at 10°C. under constant fluorescent lighting. The remainder was placed in formalin-acetic-alcohol based on 50% ethyl alcohol (Johansen 1940) for future examination and the making of permanent preparations.

(a) Associated Species.

A close examination of the plants yielded quite a lot of information on the species associated with the Pylaiella. All plants bore the blue-green epiphyte Phormidium fragile which is typically associated with the Pylaiella plants at St. Andrews.

Also present were many diatoms, chiefly Coscinodiscus concinus and a Navicula sp.. The green unicellular Entocladia viridis occurred commonly in colonies creeping up the sides of the filaments and specimens of young Enteromorpha sp., Ceramium sp., Rhodochorton sp., and Bangia fuscopurpurea were also observed.

The only animal identified was a species of Epistylis, a Vorticella-like organism.

(b) Morphology.

The morphology of P. rupincola was examined and where possible the various features were measured according to the measurements already taken for the P. littoralis at St. Andrews. The vegetative cells in the main filaments were found to have an average diameter of 30.5μ and lengths which ranged from 15.5μ to 48.5μ . In the ultimate branches the diameter of the cells was about 15μ narrowing to 12.9μ in the filament tips. The walls of the average vegetative cell were 2.3μ thick.

Unilocular sporangia were found to have the average dimensions of 31μ broad x 22μ long but again these varied considerably, in breadth for example, from 35.5μ to 24.5μ and in length from 29.6μ to 13.3μ . The sporangia were equipped with ejectory papilla which projected from the main body of the sporangium by an average of 3.5μ while the average sporangium had a wall 2.9μ in thickness. None of the plants bore any plurilocular sporangia.

Angles of Branch Emergence in Pylaiella rupincola (Aresch.) Kylin

at Kristineberg

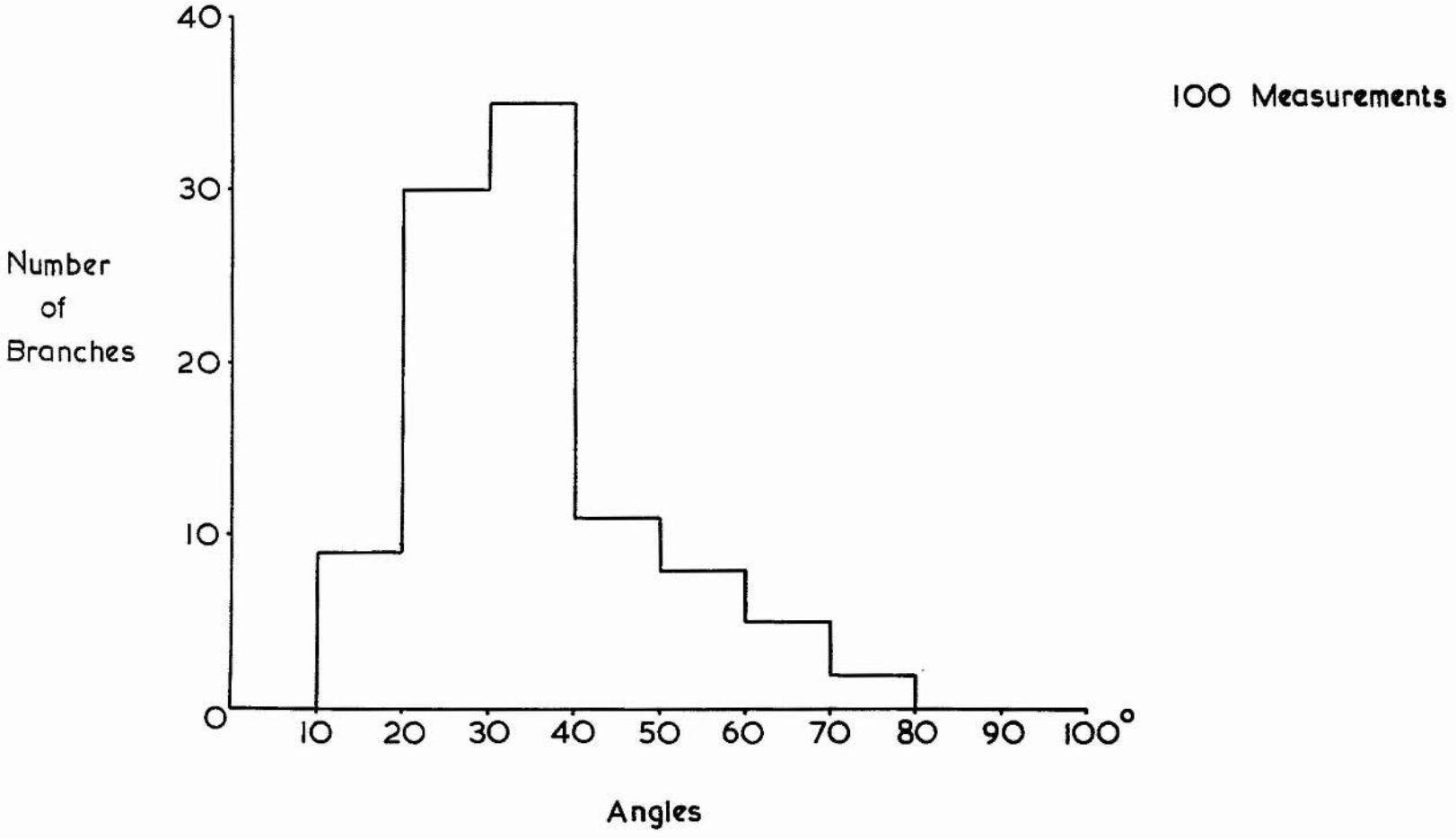


Fig. 11

The angles of branch emergence in P. rupincola were also measured. As with P. littoralis several plants were taken and one hundred branches selected at random and drawn by means of a camera lucida. The mean angle of emergence was found to be 35.4° and the actual distribution of the angles is shown in the histogram (Fig.11). This histogram is drawn to the same proportions as those used for P. littoralis and its similarity in form with that for lithophytic P. littoralis is striking.

(c) Sporangial Type.

All plants were found to bear unilocular sporangia alone.

(d) Life Cycle.

A few weeks after the live P. rupincola had been placed in culture solution it became evident that it had released zoospores, for close examination showed that the deep petri dishes contained masses of short creeping filaments. The adult material was then removed as it was now overgrown with diatoms and other algae but this was unavoidable due to the urgent nature of the setting up of the experiment. Nevertheless the young Pylaiella plants became fertile and on the 14th January, 1959 these were found to bear plurilocular sporangia only. The plants were extremely tiny and were only just visible to the naked eye (Figs. 37 and 38).

With the aid of a binocular dissecting microscope some of

these plants were disentangled from the mass of other algal filaments and transferred to fresh petri dishes, again containing the enriched Erd-Schreiber solution.

Various attempts were made to observe the plurilocular sporangia release their contents but unfortunately this was never seen. Nevertheless the plants did fruit in culture and a second generation of young Pylaiella germinated. Relative to the first generation these plants were quite large reaching a length of about one centimetre and showing much larger filament diameters with prominent cable rolling. On 23rd February these plants were found to be fertile and bearing unilocular sporangia only, or both types simultaneously (Figs.39 and 40).

X. DISCUSSION

Two features emerge as the most important from this study. The first is the evident close relationship between the distribution and the life cycle of Pylaiella littoralis, and the second the validity of Pylaiella rupincola as a separate species.

Since Knight(1923) laid down the rules for the life cycle of P. littoralis at the Isle of Man, the sequence of generations has been shown to vary considerably, at Heligoland by Damman (1930), on the West Coast of Sweden by Kylin (1933), and (1937), and again at St. Andrews in the course of the present study. It has been shown, too, in this work that the occurrence of the successive generations of P. littoralis follows a fairly regular pattern not only in the timing of their appearances but in the habitats they occupy. As these habitats are subject to different environmental conditions the problem of the algal life cycle becomes more complex and must therefore be considered from all angles and not deduced merely from, say, a cytological investigation.

The more important environmental conditions are therefore worthy of further discussion. It is evident from the graph showing seasonal fluctuations in the temperatures of inshore sea water and that illustrating the growth of lithophytic Pylaiella for the same period that the two follow one another

pretty closely. The sea temperature reached a maximum in July and fell in August but due to prolonged warm weather rose again slightly in September before dropping quickly to the winter level. This slight rise was reflected in a similar small increase in mean frond length of the Pylaiella in the same month. It would seem then that temperature is all important in the growth fluctuations of Pylaiella. Yet as Knight and Parke (1931) point out, this factor of temperature is almost impossible to separate from that of light as both tend to move in the same directions at the same time in their variations. They also argue that light is the more important since most algae show a greater acceleration in growth during very early spring when the increase both in length and intensity of daylight is often much more striking than the rise in sea temperatures.

This does not appear to be the case for the Pylaiella at St. Andrews. Lithophytic plants are at minimum size in January and show an increase in the following month. This is paralleled exactly in the sea temperatures.

At St. Andrews, too, an examination of the boulder community shows that it is in shadow from a fifty foot cliff for most of the year yet a growth of Pylaiella appears in spring and persists until the autumn just as it does on Fucus, for example, on parts of the shore exposed to full daylight.

Light therefore seems of less importance than temperature in its influence on growth.

Temperature, however, seems to have another important effect and that is upon the type of sporangia produced by the plants. Throughout the winter months almost every Pylaiella plant from any habitat will be found to bear unilocular sporangia alone, the remainder bearing both types with unilocular in the majority. The increase in temperature in very early spring, however, is accompanied by the appearance of the lithophytic gametophyte which, of course, bears plurilocular gametangia only while later in the season the epiphytic material, though sporophyte in function, bears mostly plurilocular sporangia along with a few of the unilocular type. This change is also evident in the lithophytic sporophyte population which during the summer is found with about 30% of its reproductive output directed to formation of plurilocular sporangia as opposed to less than 5% in winter.

Nevertheless there are two exceptions to this trend and these are in the Pylaiella growing on the boulders at the cliff foot and in the harbour. In both habitats the species bears unilocular sporangia exclusively throughout the growth seasons but as far as environmental conditions are concerned the habitats could hardly be more different. The former receives full wave action from normally saline sea water and suffers from

prolonged shadow while the latter receives full sunshine but contains sea water of low salinity which never becomes agitated. The most probable explanation is that prolonged shade and low salinity, like low temperature and high pH, are adverse conditions and that under such adverse conditions the sporophyte of the species tends to form unilocular sporangia.

In addition to its effect on the type of sporangia borne by the species low salinity inhibits also their production. Of all the Pylaiella examined, that growing in the harbour had consistently the lowest fertility. Sporangia were rare, were never found in chains of more than thirteen (eight being nearer the average) and were very often quite solitary. This effect of the harbour water was confirmed by the experiments involving the transplanting of material from other habitats to the harbour and by similar experiments in culture.

The low fertility of the harbour material is accompanied by an immense vegetative development. The largest Pylaiella frond measured during the investigation was 91 cms. in length and was growing in the harbour among others almost as large. As has been mentioned, the dehiscence of an intercalary sporangium weakens the filament so that eventually the part of the filament distal to the sporangium becomes detached. The low fertility of the harbour Pylaiella than automatically results in less shedding of the filaments and this, accompanied

by the extreme calm of the water, allows the plants to grow to large size.

The plants from the various communities have been examined microscopically and the microscopic features have been found to vary little from plant to plant. Branches emerge at much the same angles, sporangia have similar dimension and there are only little differences in cell diameters. Yet there are obvious differences in frond appearance among these plants and very obvious similarities in appearance between the plants from the same habitat. All harbour plants are large in size, limp and disorganized in habit and rather pale in colour. They also have a low dry weight per unit frond area ratio. The lithophytic and epiphytic plants are also very distinctive in size and general appearance. The former are short (never measure more than 5 cm. in frond length) with very prominent cable rolling bearing many short branches and are dark chocolate brown in colour. Their dry weight per unit frond area is high. Epiphytic plants are similar in colour to the lithophytic but are much larger with less prominent cable rolling and much longer branches, while their dry weight per unit frond area is intermediate between those of the lithophytic and harbour plants.

These regular differences in appearance are accompanied by differences in response to experiment. The transplant

experiments showed that neither lithophytic nor epiphytic Pylaiella could grow in the harbour and indeed very rapidly died. The harbour material was quickly torn from its anchorage in any environment other than the harbour and so observation on its adaptability could not be made. The controlled experiments in culture have confirmed that neither lithophytic nor epiphytic can grow in harbour water but have also shown that harbour material can grow and reproduce equally well in sea waters of low and normal salinities.

These results imply that the differences between the plants from the various communities are at least partially innate, and such a possibility is not necessarily invalidated by the rather anomalous harbour community. In the harbour, all Pylaiella individuals bear unilocular sporangia alone, the accessory plurilocular sporangia common to the sporophytes of epiphytic and lithophytic plants alike, are quite absent. Gametophytes have never been found in the harbour and it has been shown that a sporophyte self reproducing by zoospores from unilocular sporangia is a relative rarity for the St. Andrews Pylaiella. It is possible that a few plurilocular sporangia may be formed by harbour plants but they have never been observed and if present must be uncommon. This, however, does not necessarily mean that the harbour Pylaiella develops from zoospores released from epiphytic or lithophytic plants.

The best interpretation that can be put on the form-sporangia-environment relationship is that the different types of Pylaiella found at St. Andrews represent separate ecological races which are distinctive and constant in appearance, and which do not alter profoundly on transplanting. This statement is meant to offer a partial explanation of the variability of Pylaiella appearance and anticipates the rejection of most of the taxonomic sub-divisions. For the characters chosen by Kjellman (1890) for his subspecific taxonomy are extremely variable and his classification does not provide a usable Key for identification of such races. It is suggested, therefore, that the taxonomic unit P. littoralis should be considered as showing a potentially immense number of ecological variations and that these variations cannot be included within the system of orthodox taxonomy.

Discussion of the sporangia borne by Pylaiella leads inevitably to one on the life cycle. To anyone observing the growth of the species at St. Andrews the most striking feature is the overwhelming majority of the sporophyte plants; indeed, early on in the investigation it was thought that the gametophyte was quite absent. The development of the zoospores from unilocular sporangia in culture, however, showed that the succeeding generation bore plurilocular gametangia alone and was fertile at a very early age. The small size of these gametophytes was observed in the field where they were only

just visible to the naked eye at the upper limit of the distribution of the lithophytic plants. It is probable therefore that gametophytes of P. littoralis though uncommon are fairly widespread, at St. Andrews, but because of their tiny size and strictly seasonal (Spring) occurrence are regularly overlooked. The numerical dominance of the sporophyte is due chiefly to the fact that they are very much larger and therefore produce far more reproductive structures which in summer are predominantly sporangia of the accessory self-reproducing plurilocular type. It is also due to the heavy mortality in zoospores from unilocular sporangia. In culture about 30% of these fail to settle on the substratum and in the rough sea conditions of winter when these sporangia are chiefly formed it is probable that a higher percentage loss is obtained.

The other important feature to emerge from this study has been concerned with Pylaiella rupincola. It is evident from the results obtained that a reappraisal of its validity as a separate species is very necessary. Kylin awarded it specific status on three grounds. These were lack of alternation of generations, habit differences and morphological differences. The material on which this work has been done was sent as authentic P. rupincola from the area round Kristineberg which was also the one where Kylin worked. It

must therefore be assumed that this was his P. rupincola.

Examination of the material showed it to bear unilocular sporangia only. This fruited in culture and produced a generation of plants bearing plurilocular gametangia alone. These on isolation in fresh culture gave rise to a second generation bearing unilocular sporangia alone, or with plurilocular sporangia as well. It is, of course, unfortunate that neither zoospore nor gamete behaviour was observed and likewise the cytology was not investigated. Nevertheless, the results as they stand imply a definite alternation of generations in the pattern typical of the filamentous Ectocarpoid algae.

In habit the Pylaiella is described as growing as a sheet or carpet over rock surfaces often especially luxuriant on slightly sloping ridges. The plants are said to adjoin one another closely and never to reach a height of more than 5 cms. Morphologically they are stated to be different from P. littoralis by Kylin, but an adequate explanation of these differences is not given. The plants are supposed to be shorter and to have greater development of cable rolling than those of P. littoralis. They also, it is said, bear predominantly unilocular sporangia at all times of the year.

The described habit of P. rupincola is identical with that of the lithophytic P. littoralis at St. Andrews. The same is true for the morphology. Three thousand frond lengths

were measured in lithophytic P. littoralis over a twelve month and the longest plant was found to be 4.8 cm., the overall average being 1.8 cm. Lithophytic P. littoralis also has a greater development of cable strand than either epiphytic or any other St. Andrews material, and it reproduces mainly by means of unilocular sporangia.

The microscopic details of the morphology of P. rupincola were similarly examined. It was found that cell and sporangia dimensions were within the range for the P. littoralis at St. Andrews. The mean angle of branch emergence was 35.4° compared with 38.4° for the lithophytic P. littoralis. When the distribution of these angles was drawn in the form of a histogram, it was obvious that the pattern bore a striking resemblance to that for the lithophytic P. littoralis.

The choice then is that the lithophytic P. littoralis at St. Andrews should be now called P. rupincola or that P. rupincola (Aresch.) Kylin should once again be returned to the species P. littoralis. The latter seems preferable.

XI CONCLUSIONS

Some of the conclusions reached from this investigation have already been mentioned in the text. Others, however, have not and the more important of each are given below.

(i) It is concluded that P. littoralis is a valuable subject for autecological investigation for three reasons. First because it is one of the most common of the filamentous brown algae on the shores of the northern hemisphere. Second, because its littoral distribution, fairly large size and intercalary sporangia make it one of the easiest species in the Ectocarpaceae to identify and collect. Third, because of its variability in life cycle, habitat and form it provides an excellent subject for demonstrating the complexity and plasticity of these features in the Ectocarpaceae.

(ii) From experiments in culture and close examination in the field it is concluded that the gametophyte generation is produced from zoospores released from unilocular sporangia and occurs regularly but uncommonly in nature. Hitherto this generation has been overlooked in the field because of its near microscopic size. The life cycle at St. Andrews, therefore, is not strictly isomorphic.

(iii) The failure experienced in the present investigation to confirm completely the deduced life cycle by cytological evidence is probably due to some unknown environmental factor inhibiting nuclear division. It is concluded from the poor

evidence acquired that meiosis takes place in the development of the unilocular sporangium.

(iv) Study of the distribution of P. littoralis at St. Andrews has shown that it occupies a set of very different habitats each experiencing different environmental conditions and supporting different floras and faunas. As its appearance in most of these habitats is strictly seasonal it is concluded that the species is rather sensitive to changes in environmental conditions. Of these, wave action is the most important in actually destroying the plants, and temperature the most important factor in controlling growth rates (optimum in summer temperatures) and more dubiously in controlling the type of sporangia borne by the sporophytes (unilocular in winter and plurilocular in summer). It is concluded that light is not such an important growth stimulus as suggested by Knight and Parke (1931) but that low light intensity, like low salinity of the surrounding water, high pH and low temperature are adverse environmental conditions and that under these the sporophyte of the species tends to produce unilocular sporangia predominantly.

(v) Differences in form do occur between the Pylaiella from its various habitats, and transplant experiments in the field and in culture have shown that the different types do not react favourably to changes in environment. It is concluded then that these represent separate ecological races.

(vi) It is concluded that the award of definite taxonomic status to the many ecological races is invalid and that the existing taxonomic sub units should be re-appraised.

(vii) It is concluded that P. rupincola (Aresch.) Kylin should no longer be regarded as a separate species on the grounds postulated by Kylin, as close examination of its ecology, morphology and life cycle finds it identical with lithophytic P. littoralis (L.) Kjellm. at St. Andrews in all respects.

XII SUMMARY

(i) The nomenclature and position of Pylaiella littoralis in classifications of the Phaeophyta are briefly described, the value of the species as a subject for autecological investigation is assessed and the aims of the investigation stated.

(ii) The distribution of P. littoralis in (a) the northern hemisphere and (b) on the British coasts is reviewed and the species is found to be both common and widespread in all areas.

(iii) The morphology of P. littoralis is briefly described, the chief features being the cell wall, cell contents, cell dimensions, cable rolling, sporangia (structures and dimensions) and growth areas.

(iv) The life cycle of P. littoralis is reviewed and the findings of other workers compared with those for the species at St. Andrews. The life cycle of P. littoralis at St. Andrews is deduced from field observations, studies in culture and cytological evidence and not found to be very different from the pattern typical of the filamentous Ectocarpaceae.

(v) The stages of early growth from the zoospore to the age of six weeks are described on the basis of observations made on the species growing in culture.

(vi) The distribution of P. littoralis at St. Andrews is found to fall into several natural communities. These are

(1) a permanent lithophytic community growing on rock ridges at about mean tide level, (2) a community growing on boulders at the foot of a north-facing cliff, (3) an epiphytic community found in summer and autumn on open parts of the shore and in winter and spring in pools at, or slightly below, high water of neap tides, (4) a community growing on mud, stones or Fucus ceranoides within the confines of the harbour at St. Andrews and lastly, (5) a salt marsh community at the estuary of the River Eden some three miles to the north of St. Andrews. The different species of algae and, to a lesser extent, of fauna associated with the Pylaiella in these communities are described. The more important environmental conditions are also described and, where possible, measured. Additional information when relevant to the species in any of the communities is given in the form of short notes.

(vii) The differences between the Pylaiella plants from the three main communities (i.e. lithophytic, epiphytic and harbour) are described from morphological features and from the results of transplant experiments in the field and in culture.

(viii) The subspecific taxonomy of P. littoralis is reviewed and the plants from the three main communities at St.Andrews identified.

(ix) The life cycle, morphology and ecology of Pylaiella rupincola is reviewed and the results of a personal investigatio of the species given, the material used in the investigation

having been sent from Kristineberg, Sweden.

(x) The two main features arising from the present study are discussed. These are (1) the close relationship between distribution, environmental conditions, and life cycle in P. littoralis and (2) the validity of P. rupincola as a species separate from P. littoralis.

(xi) The various conclusions reached from the investigation are given; of these the most important are:-

(1) The gametophyte generation of P. littoralis is produced by germination of the zoospores released from unilocular sporangia. This generation is small in size, seasonal (spring) in distribution, and, relative to the sporophyte, of uncommon occurrence at St. Andrews.

(2) Environmental conditions affect the growth, fertility and the types of sporangia borne by P. littoralis but changes in the environmental conditions are not accompanied by morphological alteration and are generally detrimental to the species.

(3) The ecological races of P. littoralis cannot be described in the nomenclature of orthodox taxonomy.

(4) As a result of the investigation carried out on P. rupincola it is concluded that it should no longer be separated from P. littoralis on the grounds suggested by Kylin (1937).

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XIV. LIST OF PLATES AND ILLUSTRATIONS

Text Figures.

Fig.10. (Page 88) Histograms showing the angles of branch emergence and their distribution in three samples of P. littoralis from lithophytic, harbour and epiphytic communities respectively (100 measurements per sample).

Fig.11. (Page 108) Histograms showing angles of branch emergence in P. rupincola. The histogram is based on 100 measurements and should be compared with that for lithophytic P. littoralis (see Page 88).

PLATE I.

Fig.12. Photomicrograph of part of frond showing two zones of active cell division.

Magnification x 250.

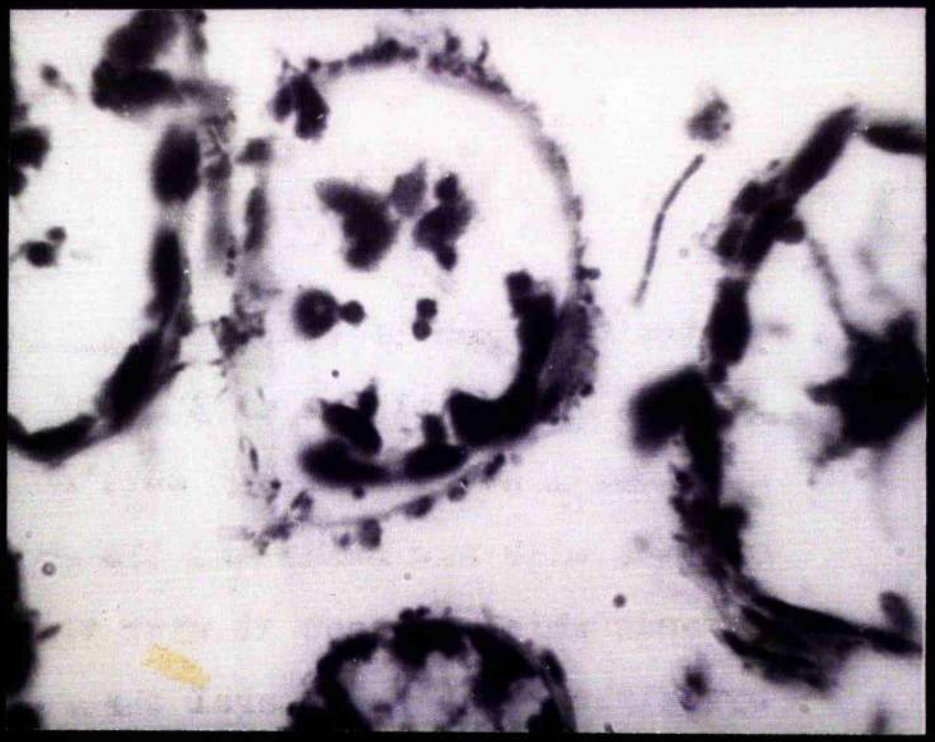
PLATE II.

Fig.13. Photomicrograph of cells of P. littoralis seen in T.S. Material cut at 3μ and stained with Heidenhain haematoxylin. Cell on R.H.S. shows nucleus with nucleolus and the cytoplasmic strands which connect it with the peripheral cytoplasm. The peripheral chromatophores can be seen. The centre cell shows chromatophores with several small spherical pyrenoids and in the cell on the L.H.S. the double nature of the wall can just be distinguished.

Magnification x 1400

Fig.14. Camera lucida drawing of two vegetative cells of P. littoralis cut in L.S. Features depicted are nucleus with nucleolus and chromatin, cytoplasmic strands, and chromatophores with pyrenoids.

Magnification x 1300



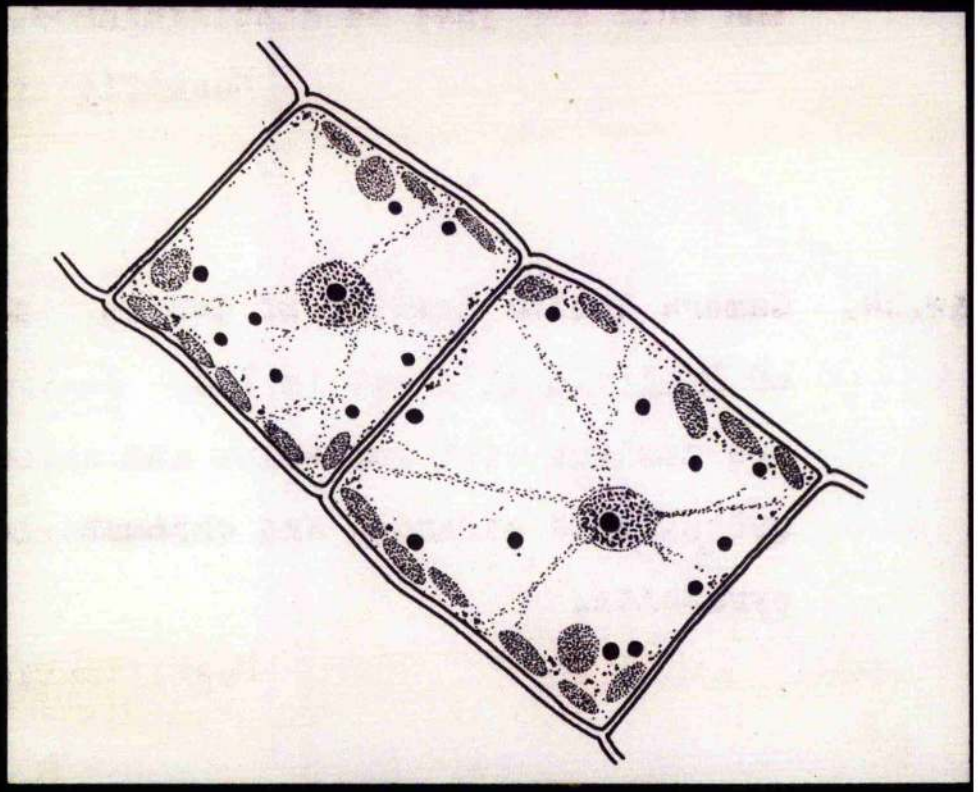


PLATE III.

Fig.15. Photomicrograph of P.littoralis showing the chains of unilocular sporangia which are borne in an intercalary position.

Magnification x 140.

Fig.16. Camera lucida drawing of three unilocular sporangia cut at 3μ and stained with Heidenhain haematoxylin. The chromatophores and pyrenoids of the developing zoospores can be seen.

Magnification x 1100.

Small illustration shows abnormal conditions in the formation of unilocular sporangia.

Magnification x 120.

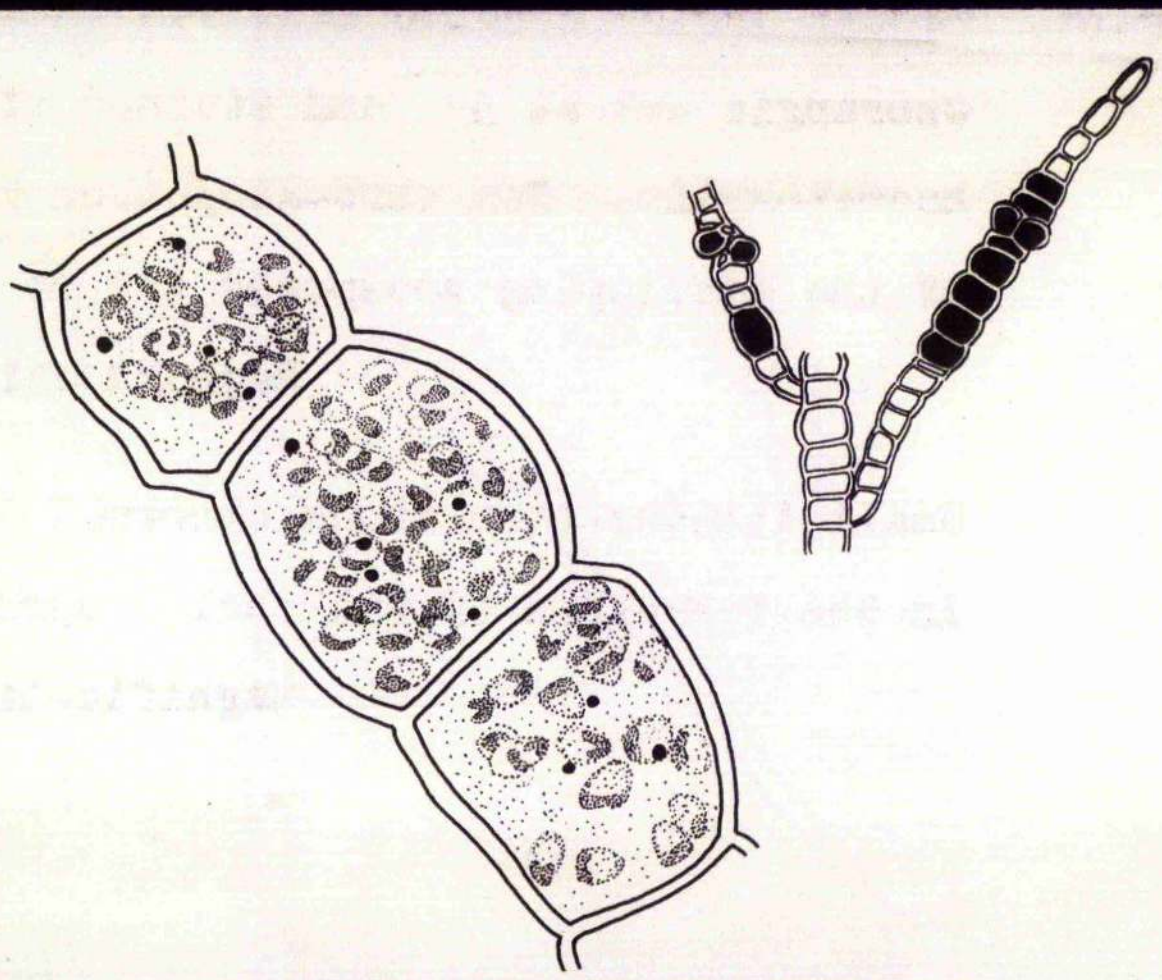


PLATE IV.

Fig.17. Photomicrograph of intercalary plurilocular sporangia on P. littoralis.

Magnification x 140.

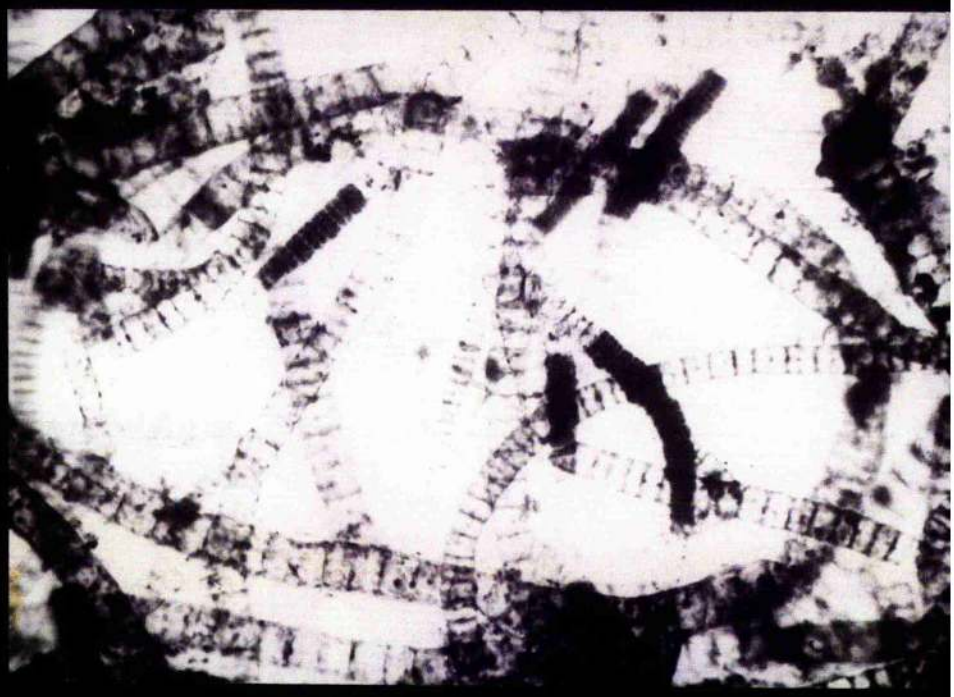


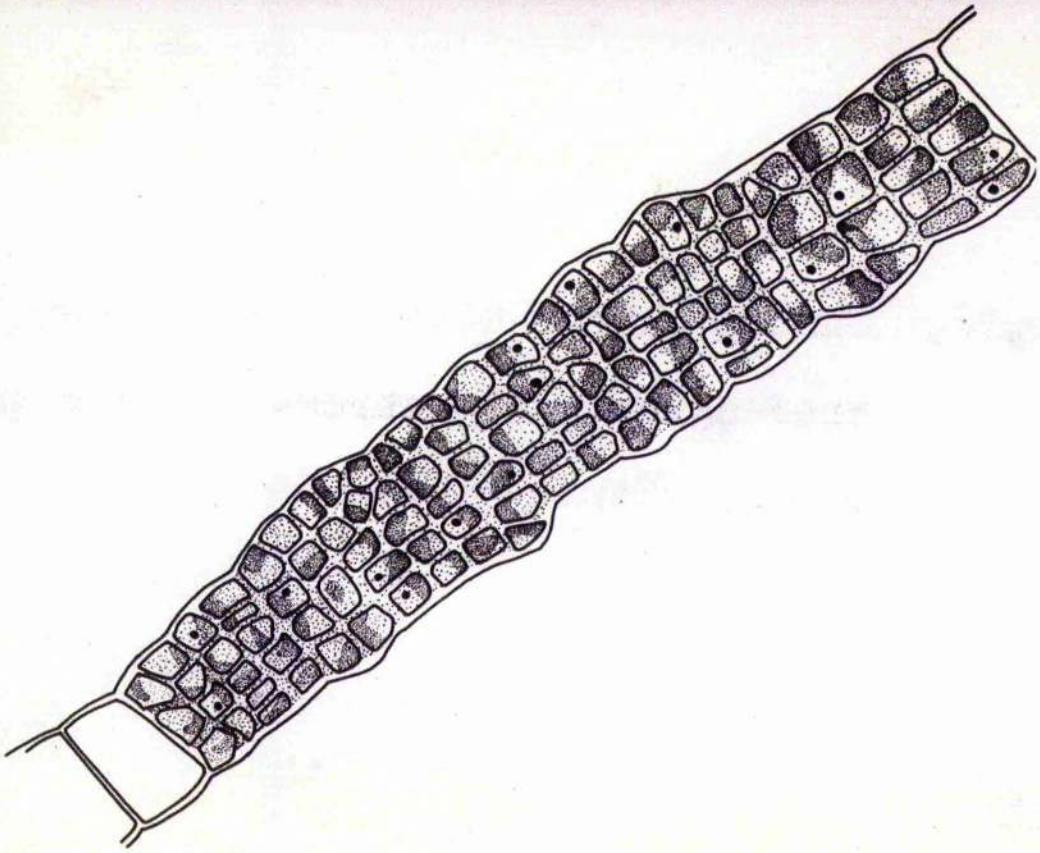
PLATE V.

Fig.18. Camera lucida drawing of intercalary plurilocular sporangium. The chromatophores and pyrenoids can be distinguished in certain of the loculi.

Magnification x 900.

Fig.19. Camera lucida drawing of plurilocular reproductive structure of sexual type. It is borne terminally.

Magnification x 1200.



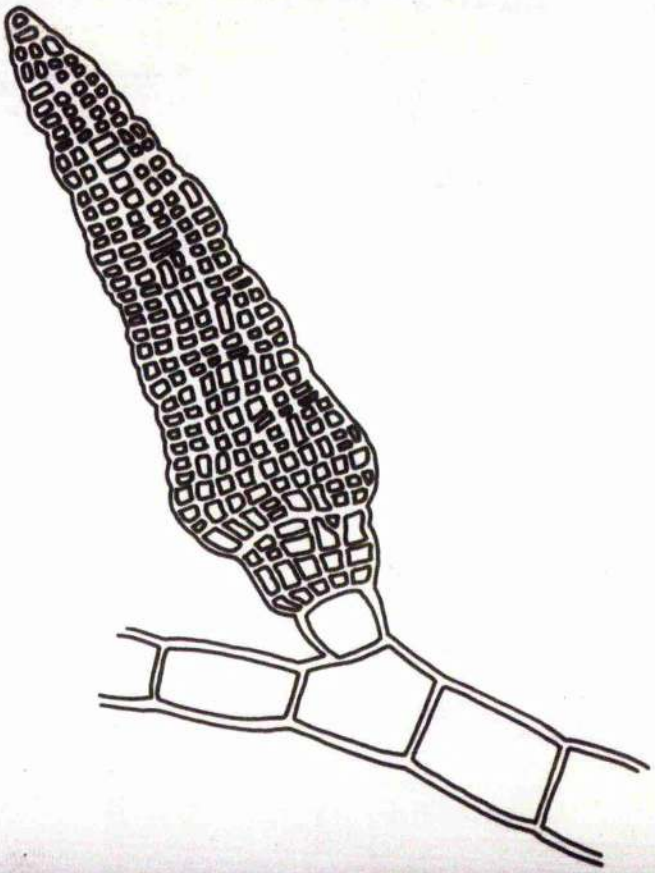


PLATE VI.

Fig.20. Photomicrograph of gametophyte of P.littoralis as it occurs in nature i.e. as a lithophyte. Several plurilocular gametangia can be seen.

Magnification x 110.

Fig.21. Camera lucida drawing of gametophyte of P. littoralis as found in nature. The gametangia are borne terminally, either on short lateral branches or short erect filaments.

Magnification x 200.

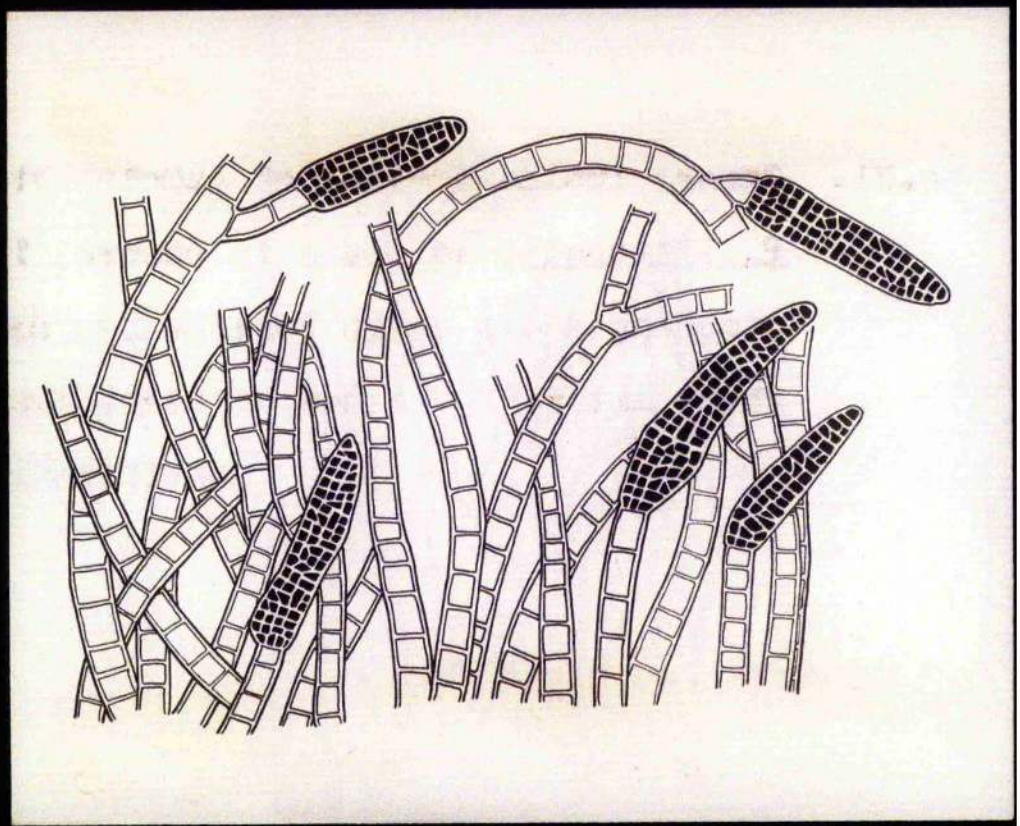


PLATE VII.

Fig.22. Photomicrograph of gametophyte of P. littoralis. The material was grown from zoospores released from unilocular sporangia and was allowed to develop in culture. Gametangia can be seen. Magnification x 300.

Fig.23. Camera lucida drawing of part of above. Magnification x 900.

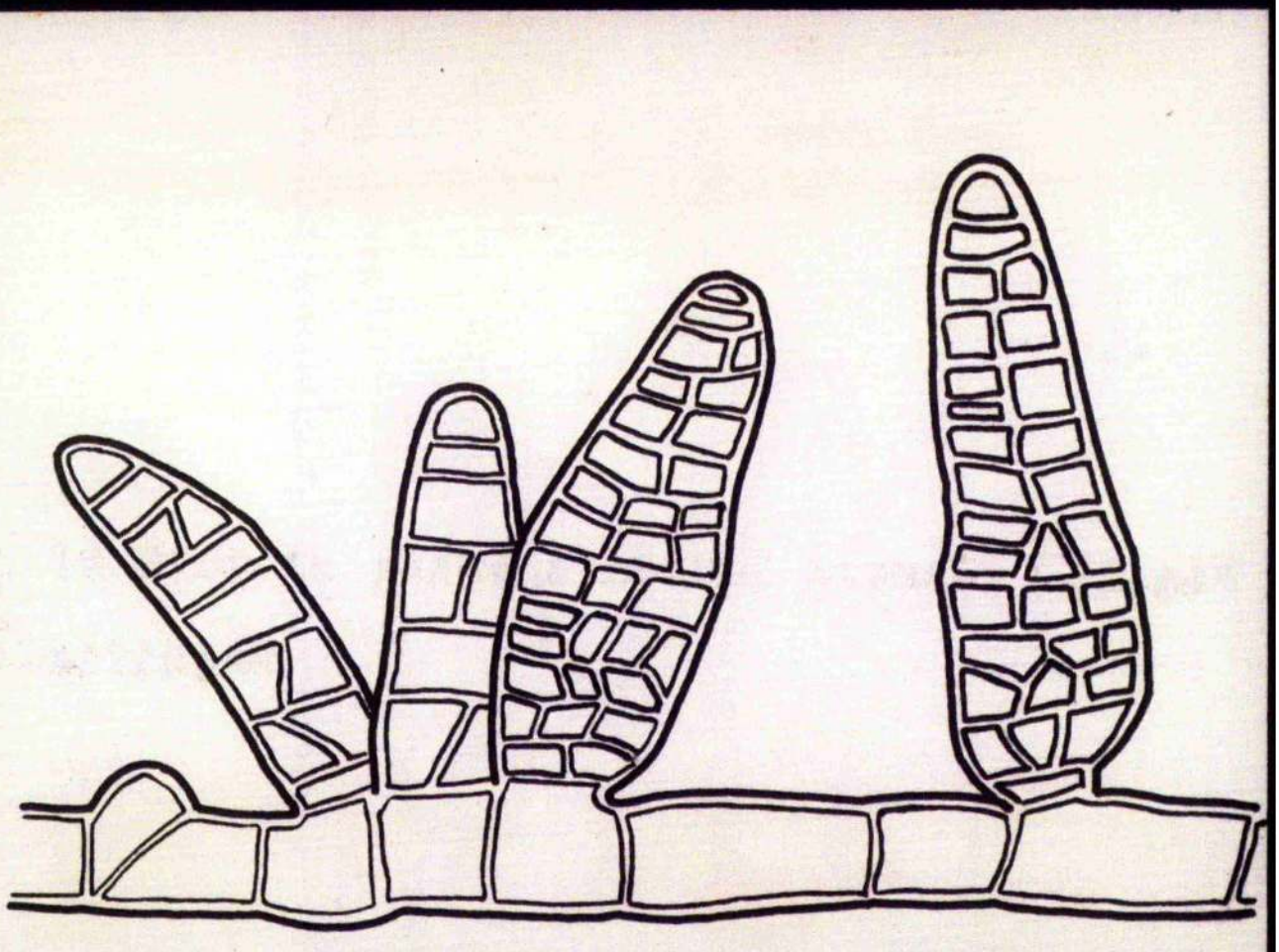


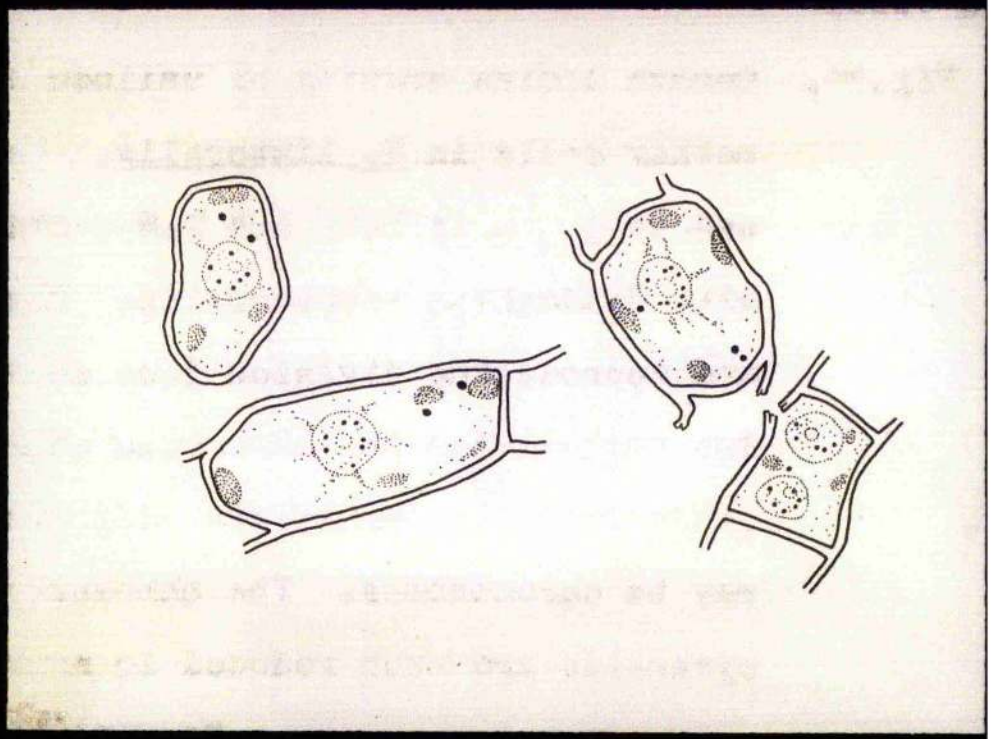
PLATE VIII.

Fig.24. Camera lucida drawing of unilocular sporangia mother cells in P. littoralis. Material was cut at 3μ , in L.S. and T.S., and stained with Heidenhain haematoxylin. The nuclei are approaching division (one cell contains two nuclei) and the chromatin can be seen condensed into darkly staining granules which may be chromosomes. The chromatophores and pyrenoids are much reduced in number.

Magnification x 1000.

Fig.25. Camera lucida drawing of zoospores. Eye-spots, nuclei, chromatophores and pyrenoids can be seen with direct illumination. With dark-background illumination the flagella are clearly visible.

Magnification x 3,500.



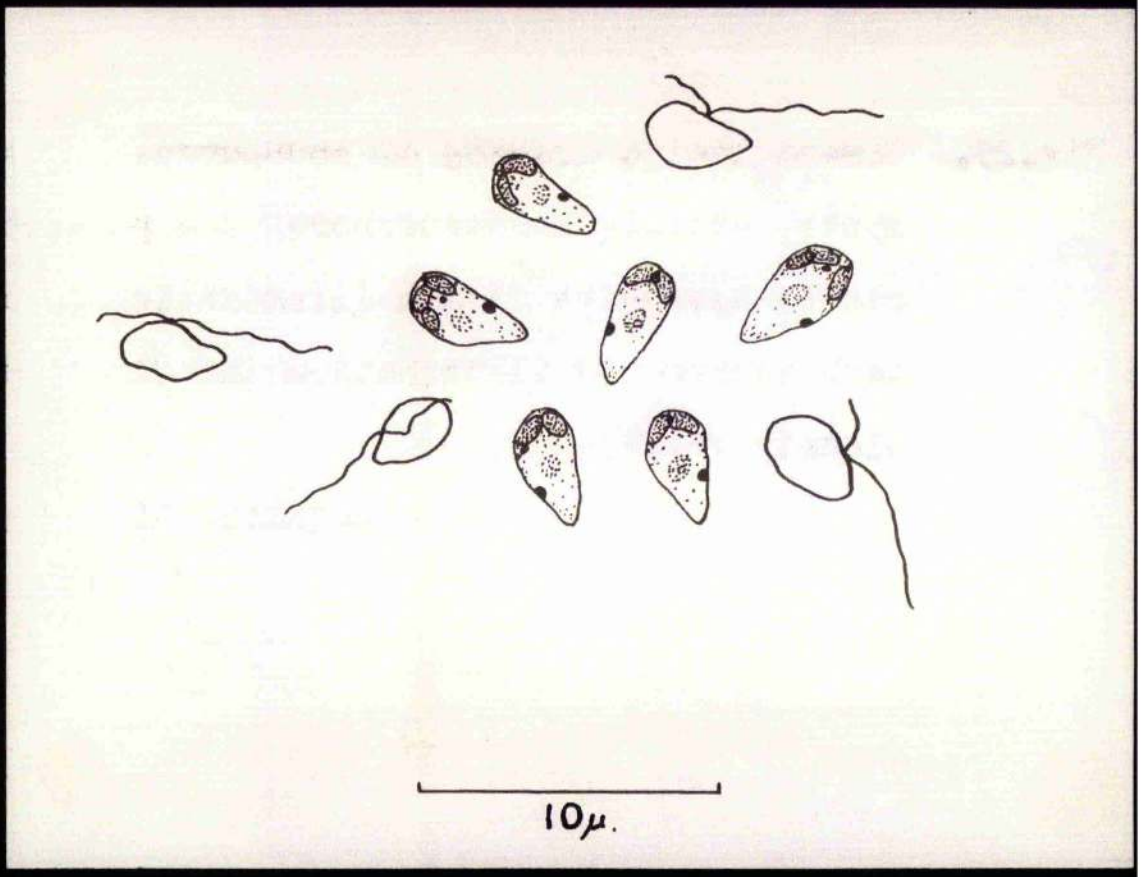

10μ.

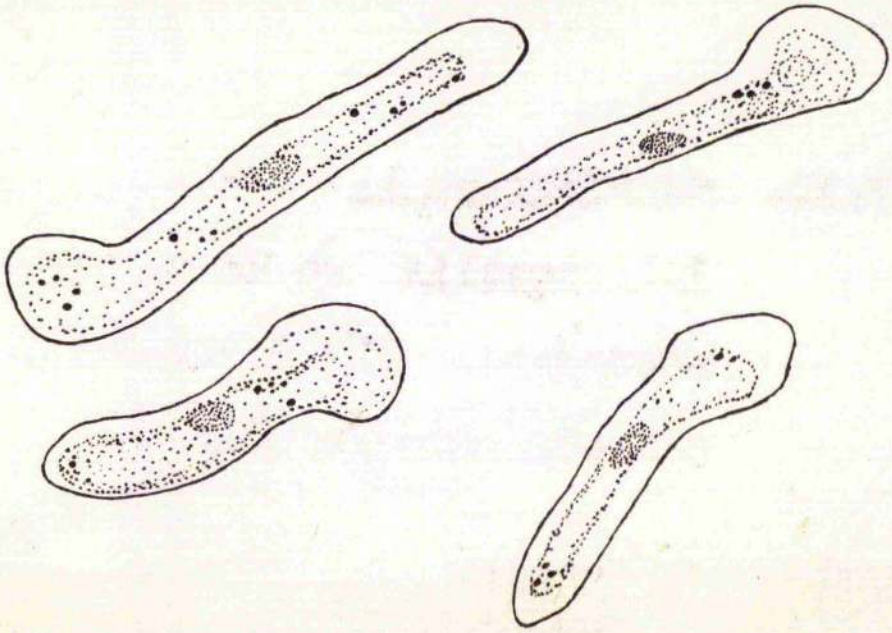
PLATE IX.

Fig.26. Germination 1. Camera lucida drawing of P.littoralis 24 hours after settling of zoospores. The germination tubes have already been formed.

Magnification x 1800.

Fig.27. Germination 2. Camera lucida drawing of young plant after one week's growth. Two short erect filaments have been produced and the basal portion consists of 10 cells.

Magnification x 500.



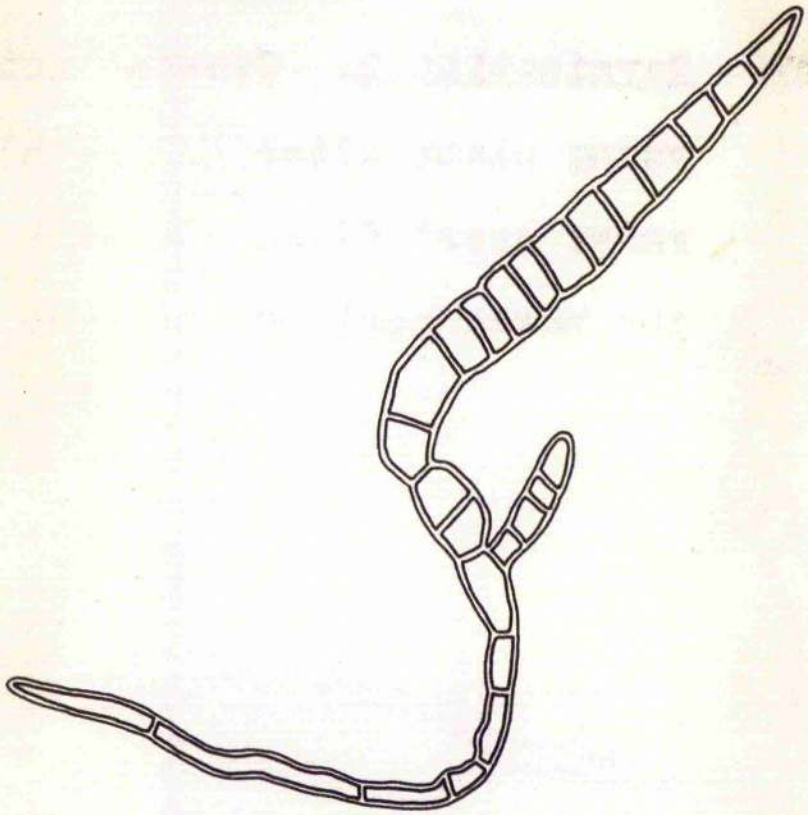


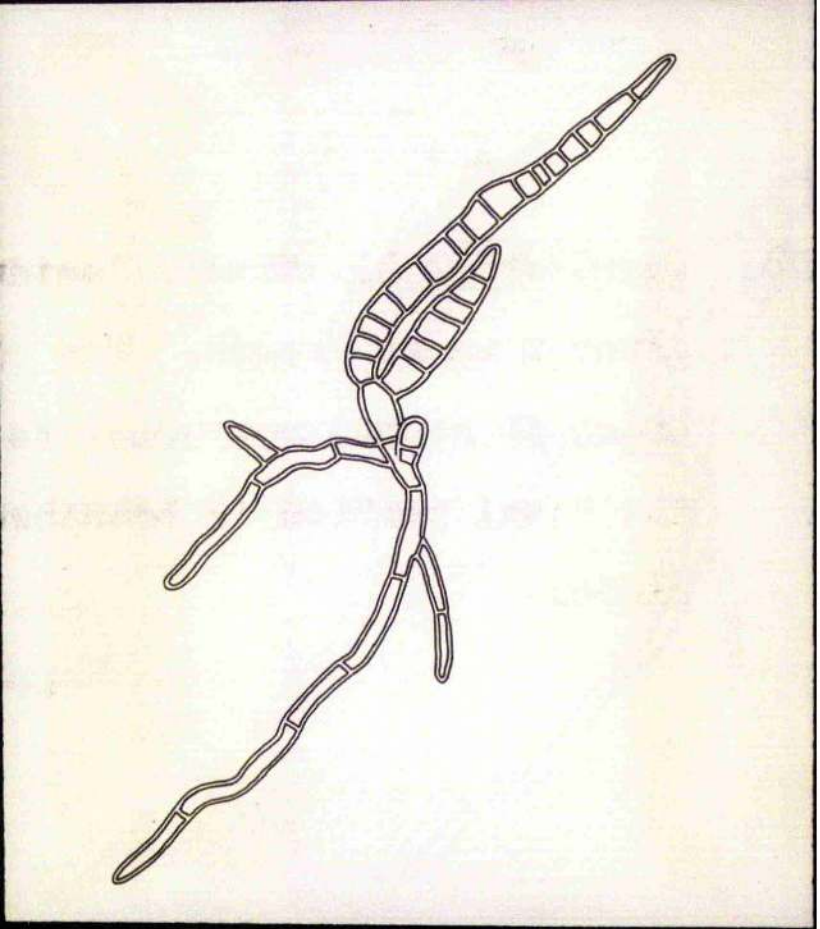
PLATE X.

Fig.28. Germination 3. Camera lucida drawing of plant after 2 weeks growth. The oldest of the erect filaments now consists of 16 cells and the basal portion is branched in several places.

Magnification x 300.

Fig.29. Germination 4. Camera lucida drawing of plant after 3 weeks. Erect filaments are being produced in large numbers and both erect and basal systems are branched. Growth in the erect system now exceeds that in the prostrate.

Magnification x 120.



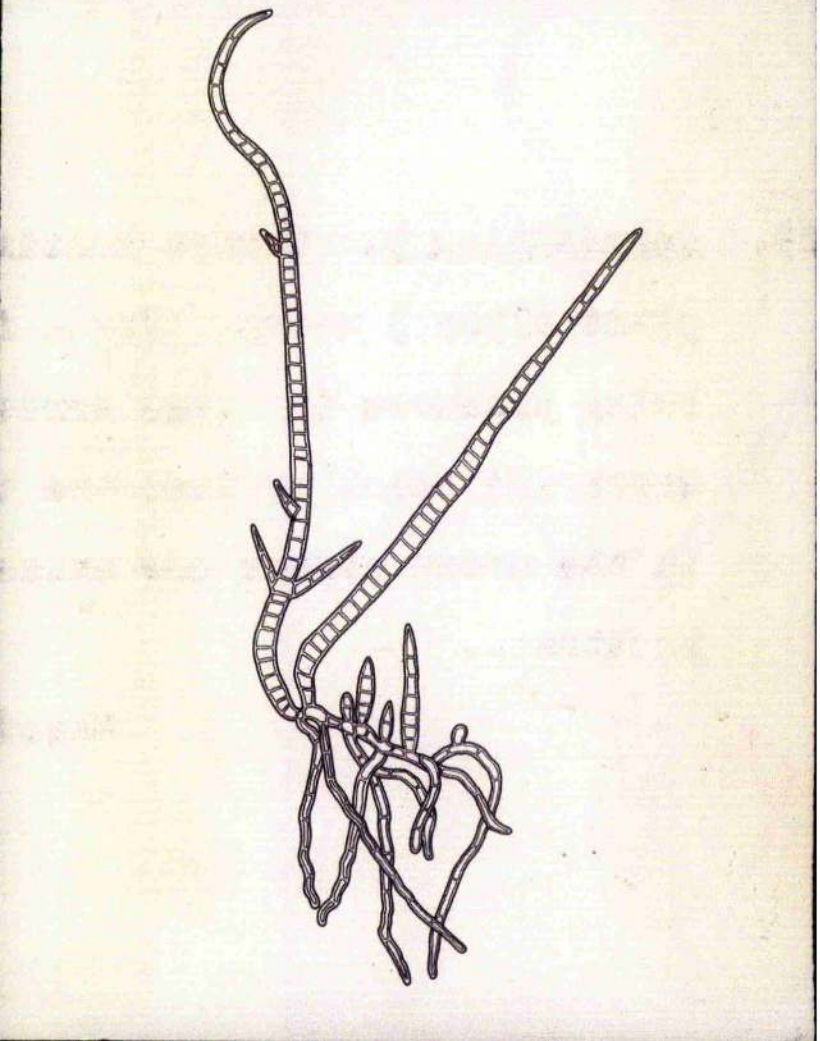


PLATE XI.

Fig.30. Photograph of lithophytic *P. littoralis* growing among fronds of *Fucus vesiculosus*.

Fig.31. Photograph of rock surface bearing *P. littoralis* and showing effect of wave action on the sandstone.

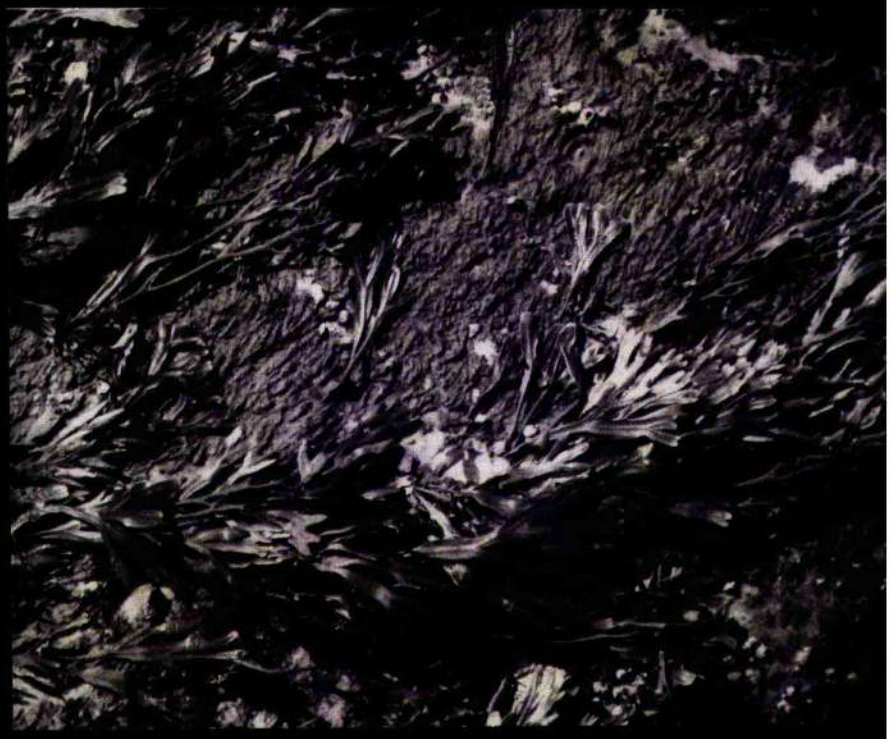


PLATE XII.

Fig.32. Photograph of some of the large boulders which bear one of the *P. littoralis* communities at St. Andrews.

PLATE XIII.

Fig.33. Photograph of P. littoralis growing epiphytically on Fucus vesiculosus. This is typical of epiphytic Pylaiella in the summer-autumn phase of its distribution;

Fig.34. Photograph of P. littoralis growing epiphytically on Fucus vesiculosus in a pool at H.W.N.T. This is typical of epiphytic Pylaiella in winter and spring.

PLATE XIV.

Fig.35. Photograph of P. littoralis growing among Fucus ceranoides on the mud of the harbour at St. Andrews.

Fig.36. Photograph of a salt pan in the salt marsh community. Some of the free-living algae can be seen entangled with one another and with the roots and rhizomes of Festuca rubra.

PLATE XV.

Fig.37. Photomicrograph of gametophyte of P. rupincola showing gametangia.

Magnification x 275.

Fig.38. Camera lucida drawing of gametophyte of P. rupincola.

Magnification x 490

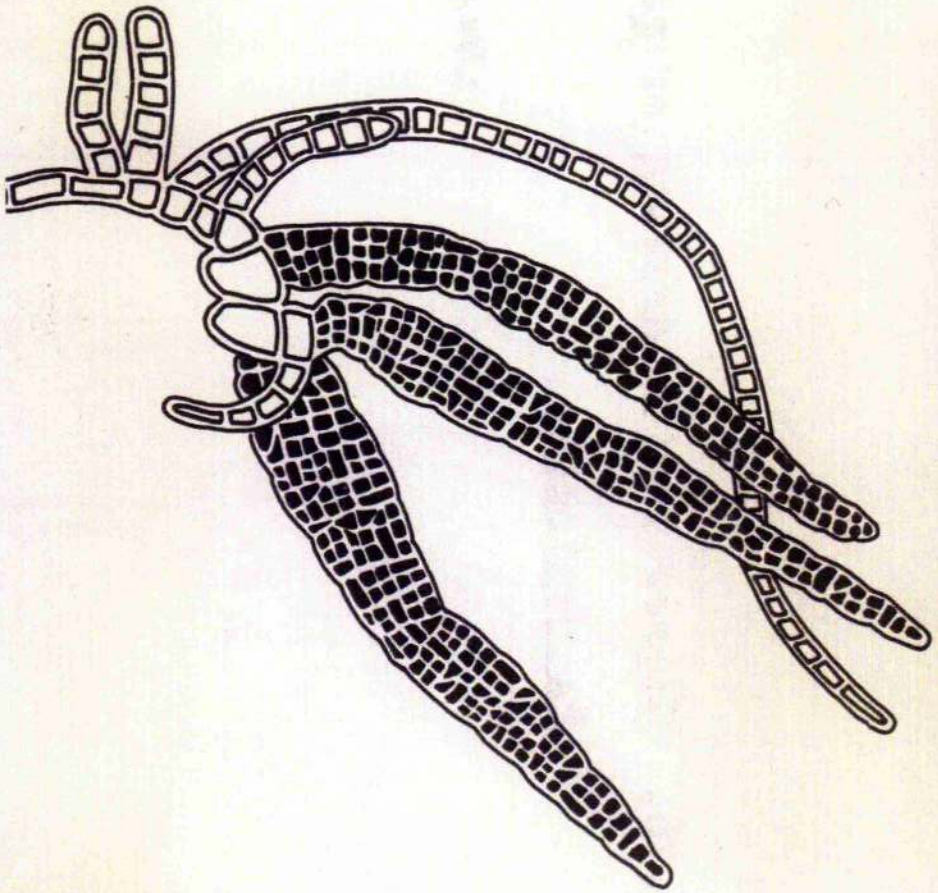


PLATE XVI.

Fig.39. Photomicrograph showing part of second sporophyte generation of P. rupincola. Unilocular sporangia are visible.

Magnification x 170.

Fig.40. Camera lucida drawing of part of second sporophyte generation of P. rupincola bearing unilocular sporangia.

Magnification x 420.